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Neotropical Monogenoidea. 18. *Anacanthorus* Mizelle and Price, 1965 (Dactylogyridae, Anacanthorinae) of Piranha (Characoidea, Serrasalmidae) from the Central Amazon, their Phylogeny, and Aspects of Host–Parasite Coevolution

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ABSTRACT: Thirteen new species of *Anacanthorus* are described from the gills of 9 piranha species from the central Amazon: *Anacanthorus amazonicus* sp. n. from *Serrasalmus rhombeus* (Linnaeus), *Serrasalmus* sp. (2 of Jégu), and *Pristobrycon striolatus* (Steindachner); *A. cinctus* sp. n., *A. crytocaulus* sp. n., and *A. lasiophallus* sp. n. from *P. striolatus*; *A. cladophallus* sp. n. and *A. scapanus* sp. n. from *S. spilopleura* Kner; *A. gravihamulatus* sp. n. from *S. rhombeus, Serrasalmus* sp. (2 of Jégu), and *P. eigenmanni* (Norman); *A. jegui* sp. n. from *S. rhombeus*; *A. mesocondylus* sp. n. from *S. elongatus* Kner, *S. rhombeus, S. spilopleura, Serrasalmus* sp. (1 of Jégu), *Serrasalmus* sp. (2 of Jégu), *P. eigenmanni,* and *Pristobrycon* sp.; *A. prodigiosus* sp. n. from *S. elongatus, S. rhombeus, Serrasalmus* sp. (1 of Jégu), and *Serrasalmus* sp. (2 of Jégu); *A. ramosissimus* sp. n. from *S. elongatus*; *A. sciponophallus* sp. n. from *S. elongatus, S. rhombeus, S. spilopleura, Serrasalmus* sp. (2n = 58), *Serrasalmus* sp. (1 of Jégu), and *Serrasalmus* sp. (2 of Jégu); and *A. serrasalmi* sp. n. from *S. elongatus, S. rhombeus, Serrasalmus* sp. (2n = 58), *Serrasalmus* sp. (1 of Jégu), and *Serrasalmus* sp. (2 of Jégu). Utilizing 12 homologous series comprising 28 character states, a hypothesis for the phylogeny of 22 central Amazonian species of *Anacanthorus* from piranha is proposed. Monophyly of the ingroup is supported by 2 synapomorphies: a cirrus with a tendency to curl into J-shaped configurations and an accessory piece nonarticulated to the cirral base. Based on parasite data, a preliminary hypothesis for the phylogeny of 10 species of piranha (Serrasalmidae) in *Pygocentrus, Pristobrycon,* and *Serrasalmus* is proposed. The host cladogram indicates that *Serrasalmus* and *Pristobrycon* are paraphyletic. A parasite–host list of *Anacanthorus* species is provided.

KEY WORDS: Brazil, taxonomy, Monogenoidea, Dactylogyridae, Anacanthorinae, cladistics, coevolution, piranha, *Anacanthorus amazonicus* sp. n., *Anacanthorus cinctus* sp. n., *Anacanthorus cladophallus* sp. n., *Anacanthorus crytocaulus* sp. n., *Anacanthorus gravihamulatus* sp. n., *Anacanthorus jegui* sp. n., *Anacanthorus lasiophallus* sp. n., *Anacanthorus mesocondylus* sp. n., *Anacanthorus prodigiosus* sp. n., *Anacanthorus ramosissimus* sp. n., *Anacanthorus scapanus* sp. n., *Anacanthorus sciponophallus* sp. n., *Anacanthorus serrasalmi* sp. n., *Anacanthorus stachophallus, Anacanthorus thatcheri, Anacanthorus palamophallus, Anacanthorus periphallus, Anacanthorus mastigophallus, Anacanthorus reginae, Anacanthorus beleophallus, Anacanthorus xaniophallus, Anacanthorus lepyrophallus, Serrasalmus rhombeus, Serrasalmus elongatus, Serrasalmus spilopleura, Serrasalmus* sp., *Pristobrycon striolatus, Pristobrycon eigenmanni, Pristobrycon* sp., *Pygocentrus nattereri,* Serrasalmidae.

The Serrasalmidae consists of 13 genera of characoid fishes endemic to South America. Included in this family are *Pygopristis, Pygocentrus, Pristobrycon,* and *Serrasalmus,* which make up the popular and often publicized group referred to as "piranha." Species from 2 of these, *Pygocentrus* and *Serrasalmus,* are notorious for their occasional threat to man. The creative legendry concerning the habits of these fishes far exceeds our knowledge of their ecology, behavior, and systematics. Myers (1972), Fink and Fink (1979), and Goulding (1980) indicate that the classification of piranhas is confusing, with species identification often difficult. This is evidenced by several undescribed piranha in our collections that have been provisionally identified as *Serrasalmus* sp. 1, *Serrasalmus* sp. 2, *Serrasalmus* sp. (karyotypic form 2n = 58), and *Pristobrycon* sp. by Michel Jégu, ORSTOM, INPA, Manaus, Amazonas, Brazil. Although a phylogenetic hypothesis for the serrasalmid genera has been proposed by Machado-Allison (1983), virtually nothing is known concerning evolutionary relationships of these hosts at the species level. Further, only *Pygocentrus nattereri* Kner has had its monogenoidean fauna documented (Mizelle and Price, 1965; Boeger and Kritsky, 1988; Kritsky et al., 1988). Twenty-four species comprising 7 genera of Dactylogyridae have been described from this host.

Boeger and Kritsky (1988) suggest that the Monogenoidea of *Pygocentrus nattereri* comprise monophyletic groups that may provide useful models for testing hypotheses on coevolution and biogeography. Additionally, Brooks (1981) and O'Grady and Deets (1987) have shown that

in the absence of a host phylogeny, host relationships can be derived by using their parasites as characters. The latter is accomplished by first determining phylogenetic relationships of the parasites, and then converting the parasite cladogram into a multistate character tree that reflects the genealogical relationships of the hosts. The objectives of this study were to (1) describe new species of *Anacanthorus* infesting 6 species of *Serrasalmus* and 3 species of *Pristobrycon*; (2) propose a phylogeny for the *Anacanthorus* species parasitizing these hosts and *Pygocentrus nattereri* in the central Amazon; and (3) develop a phylogenetic hypothesis for these serrasalmid hosts using the anacanthorine parasites as indicators of host evolution.

Materials and Methods

Fish hosts were collected from central Amazonia during 1984–1989. Methods of parasite collection, preparation of helminths for study, measurement and illustration are those of Kritsky et al. (1986, 1992). Measurements, all in micrometers, represent straight-line distances between extreme points and are expressed as the average followed by the range and number of specimens measured in parentheses; body length includes that of the haptor. Hook numbering is according to Mizelle (1936) (see Mizelle and Price, 1963). Generic characters are those given in an emended diagnosis by Kritsky et al. (1992). Type specimens collected from the type host were used exclusively for development of species descriptions. Type specimens and vouchers (specimens collected from other hosts) were deposited in the collections of the Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA); the U.S. National Museum, Beltsville, Maryland (USNM); the University of Nebraska State Museum, Lincoln, Nebraska (HWML); the Instituto Oswaldo Cruz, Rio de Janeiro, Brazil (IOC); and the Zoological Institute, U.S.S.R. Academy of Sciences, Leningrad (ZIAC), as indicated in the respective descriptions. Museum numbers have not been received from IOC and ZIAC for publication. For comparative purposes, the following type and voucher specimens were also examined: Holotype, *Anacanthorus anacanthorus* Mizelle and Price, 1965 (USNM 60459); holotype, 4 paratypes, *A. beleophallus* Kritsky et al., 1992 (INPA PA350, USNM 81669, HWML 33343); holotype, *A. brazilensis* Mizelle and Price, 1965 (USNM 60460); holotype, 31 paratypes, *A. catoprioni* Kritsky et al., 1992 (INPA PA354, USNM 81677, 81678, HWML 33347); holotype, 2 paratypes, *A. hoplophallus* Kritsky et al., 1992 (INPA PA363, USNM 81695); holotype, 38 paratypes, *A. lepyrophallus* Kritsky et al., 1992 (INPA PA364, USNM 81704, HWML 33362); holotype, 7 paratypes, *A. mastigophallus* Kritsky et al., 1992 (INPA PA366, USNM 81709, 81710, HWML 33363); holotype, *A. neotropicalis* Mizelle and Price, 1965 (USNM 60461); holotype, 25 paratypes, *A. palamophallus* Kritsky et al., 1992 (INPA PA368, USNM 81712, 81713, HWML 33365); holotype, 6 paratypes, *A. paraspathulatus* Kritsky et al., 1992 (INPA PA369, USNM 81714, HWML 33366); holotype, 18 paratypes, *A. pedanophallus* Kritsky et al., 1992 (INPA PA370, USNM 81715, HWML 33367); holotype, 7 paratypes, *A. periphallus* Kritsky et al., 1992 (INPA PA372, USNM 81718, 81719, HWML 33369); 67 vouchers, *A. reginae* Boeger and Kritsky, 1988 (USNM 81799, 81800); 17 vouchers, *A. spathulatus* Kritsky et al., 1979 (USNM 81798); holotype, 11 paratypes, *A. spinatus* Kritsky et al., 1992 (INPA PA376, USNM 81726, HWML 33373); holotype, 6 paratypes, *A. stachophallus* Kritsky et al., 1992 (INPA PA377, USNM 79197, 81727, HWML 23371); holotype, 11 paratypes, *A. stagmophallus* Kritsky et al., 1992 (INPA PA378, USNM 81728, HWML 33375); 139 vouchers, *A. thatcheri* Boeger and Kritsky, 1988 (USNM 81797); holotype, 91 paratypes, *A. xaniophallus* Kritsky et al., 1992 (INPA PA381, USNM 81737, 81738, HWML 33378).

An initial hypothesis on the evolutionary relationships of the species of *Anacanthorus* parasitizing 10 serrasalmid fishes was constructed using Hennigian argumentation (Hennig, 1966; Wiley, 1981) and tested with Phylogenetic Analysis Using Parsimony (PAUP) (D. L. Swofford, Illinois Natural History Survey, Champaign). Twenty-eight character states comprising 12 homologous series were utilized in the analysis. Polarization was initially determined by outgroup comparison and optimized according to procedures described by Watrous and Wheeler (1981) and Maddison et al. (1984); functional outgroups as defined by Watrous and Wheeler (1981) were used when character states were totally within the ingroup. Outgroups included *A. catoprioni, A. spathulatus, A. paraspathulatus,* and the *Anacanthorus*-species group from *Triportheus* spp. described by Kritsky et al. (1992).

The host phylogeny was generated utilizing the methods of Brooks (1981, 1990), Cressey et al. (1983), and O'Grady and Deets (1987). An additive binary-coded matrix of the parasite cladogram was constructed by mapping each host onto their respective parasite taxa. Since all hosts utilized in the analysis harbored more than 1 parasite species (Fig. 1) and no prior host phylogeny at the species level was available, this matrix was compressed via inclusive ORing (O'Grady and Deets, 1987, and Brooks, 1990) and subjected to PAUP analysis for development of the hypothesis. Parasite species representing less than 2% of the total specimens collected from a host were considered potential accidental occurrences and were not used in the analysis (Fig. 1).

Results

Dactylogyridae Bychowsky, 1933

Anacanthorinae Price, 1967

Anacanthorus Mizelle and Price, 1965 (emended, Kritsky et al., 1992)

Anacanthorus cladophallus sp. n. (Figs. 2, 10–12)

TYPE HOST AND LOCALITY: *Serrasalmus spilopleura* Kner, Rio Solimões near Ilha da Mar-

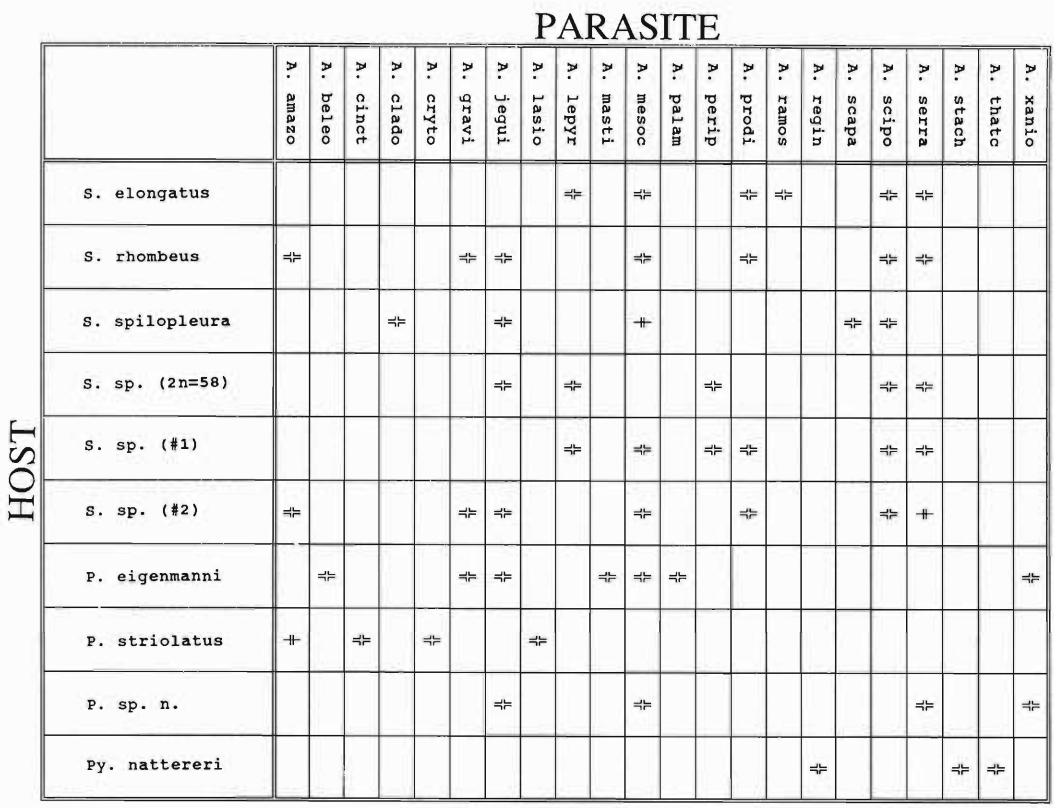


Figure 1. The occurrence of 22 species of *Anacanthorus* on their piranha hosts. ⋕ = parasites that were considered potentially accidental occurrences representing less than 2% of the total assemblage from each host and were not used in host phylogeny reconstruction. *S.* = *Serrasalmus, P.* = *Pristobrycon, Py.* = *Pygocentrus.*

chantaria, Manaus, Amazonas, Brazil (14 September 1984, 26 November 1984).

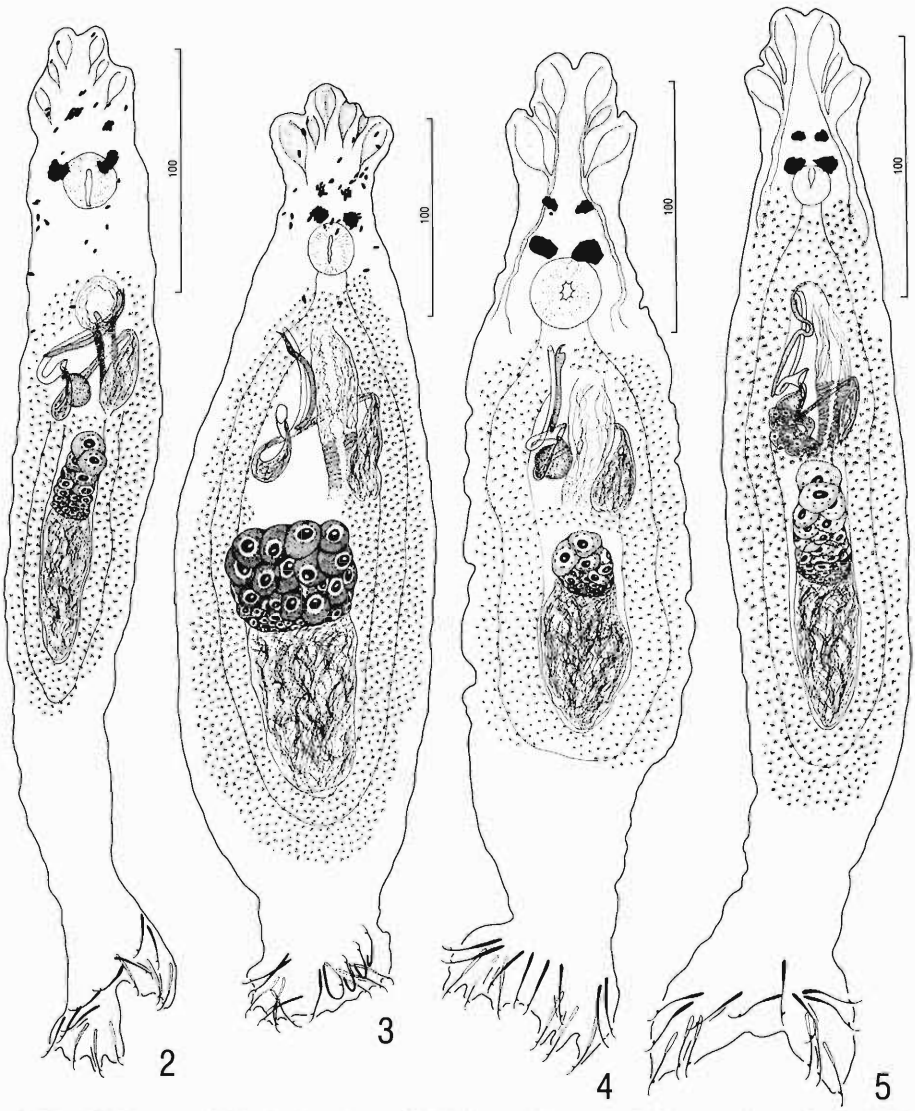
TYPE SPECIMENS: Holotype, INPA PA334; paratypes, USNM 81739, HWML 33379.

DESCRIPTION (based on 49 specimens): Body fusiform, 359 (238–542; $N = 21$) long; greatest width 74 (59–90; $N = 21$) near midlength or in anterior half. Cephalic lobes moderately developed. Four eyes, equidistant; anterior eyes frequently dissociated, smaller than posterior eyes; granules elongate ovate, large; accessory granules scattered in anterior trunk, cephalic area. Pharynx spherical to subspherical, 24 (21–28; $N = 22$) in diameter. Haptor 39 (31–49; $N = 12$) long, 63 (56–81; $N = 13$) wide. Hooks similar; each with slightly depressed thumb, shank expanded proximally; hook pairs 3, 4: 27 (25–28; $N = 19$) long, proximal expansion about 0.5 shank length; pairs 1, 2, 5–7: 22 (20–24; $N = 41$) long, proximal expansion about 0.4 shank length; filamentous hooklet (FH) loop approximately 0.5 shank length. 4A's similar, each 13 (12–14; $N = 11$), proximally expanded about 0.4 length. Gonads slightly overlapping; testis 55 (35–70; $N = 12$) × 29 (21–39; $N = 12$); ovary 33 (22–41; $N = 12$) × 22 (17–32; $N = 12$). Cirrus, accessory piece nonarticulated. Cirrus 54 (46–60; $N = 29$) long, J-shaped, with small basal flap, slight terminal thickening of wall of shaft. Accessory piece 48 (42–56; $N = 31$) long, rod-shaped, with acute distal termination, submedial (muscle) articulation point expanded forming a broad branch.

REMARKS: *Anacanthorus cladophallus* is sister species to *A. ramosissimus* sp. n. (Fig. 70). It differs from this species by having a shorter proximal expansion of the shank on hook pairs 3 and 4. The specific name is from Greek (*klados* = a branch + *phallos* = penis).

Anacanthorus scapanus sp. n. (Figs. 3, 13–15)

TYPE HOST AND LOCALITY: *Serrasalmus spilopleura* Kner, Rio Solimões near Ilha da Mar-

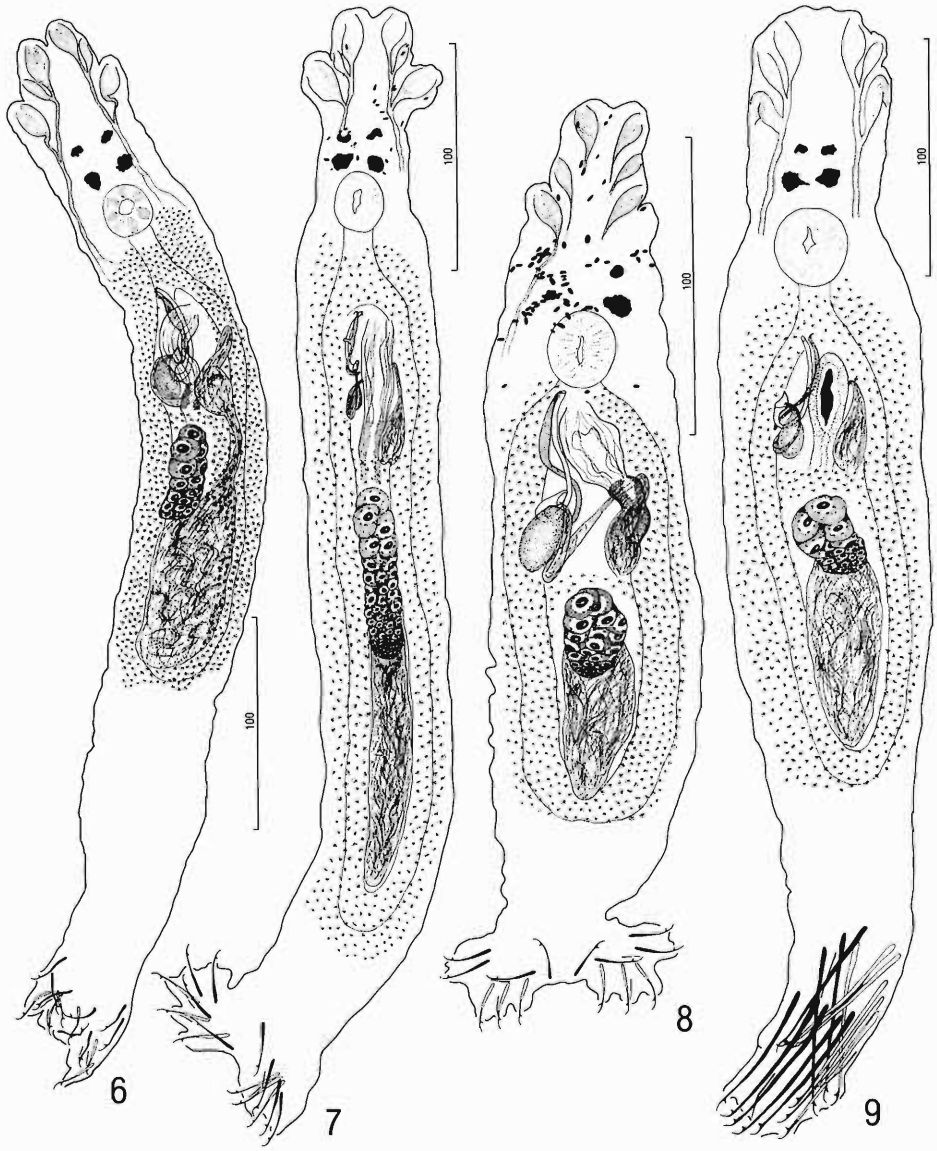


Figures 2–5. Whole mount illustrations (ventral) of *Anacanthorus* spp. 2. *Anacanthorus cladophallus* (holotype). 3. *Anacanthorus scapanus* (holotype). 4. *Anacanthorus amazonicus* (holotype). 5. *Anacanthorus crytocaulus* (holotype).

chantaria, Manaus, Amazonas, Brazil (14 September 1984).

TYPE SPECIMENS: Holotype, INPA PA335; paratypes, USNM 81740, HWML 33380.

DESCRIPTION (based on 6 specimens): Body fusiform, 487 (470–503; $N = 2$) long; greatest width 133 (130–136; $N = 2$) near midlength. Cephalic lobes well developed. Four eyes; anterior eyes occasionally dissociated; members of posterior pair larger, farther apart than those of anterior pair; granules large, elongate ovate; accessory granules peripharyngeal, scattered in cephalic area. Pharynx subspherical, 26–27 ($N = 2$) in diameter. Haptor 39 (38–40; $N = 2$) long, 77 (76–78; $N = 2$) wide. Hooks similar; each with slightly depressed thumb, shank expanded proximally; hook pairs 2–4, 6, 7: 32 (31–34; $N = 9$) long, proximal expansion 0.6 shank length; pairs 1, 5: 30 ($N = 1$) long, proximal expansion 0.5 shank length; FH loop approximately 0.4 shank length.



Figures 6–9. Whole mount illustrations (ventral) of *Anacanthorus* spp. 6. *Anacanthorus jegui* (holotype). 7. *Anacanthorus ramosissimus* (holotype). 8. *Anacanthorus serrasalmi* (holotype). 9. *Anacanthorus gravihamulatus* (holotype).

4A's similar; each 15–16 ($N = 2$) long, proximal expansion about 0.5 length. Gonads slightly overlapping; testis 90 ($N = 1$) × 51 ($N = 1$); ovary 58 (57–59; $N = 2$) × 62 (60–63; $N = 2$). Cirrus, accessory piece nonarticulating. Cirrus 53 (49–57; $N = 6$) long, broadly J-shaped, basal flap with smooth margins, slight terminal thickening of shaft wall. Accessory piece 45 (44–47; $N = 4$) long, slender, rod-shaped, with small subterminal expansion, acute distal termination; submedial (muscle) articulation point indistinct.

REMARKS: Based on the comparative morphology of the copulatory complex, *Anacanthorus scapanus* is similar to *A. serrasalmi* sp. n. It differs from this species by having hooks with longer proximal bases and by lacking a median

Table 1. Comparative measurements (in micrometers; mean with range in parentheses) of *Anacanthorus amazonicus* from 3 piranha hosts.

	*Serrasalmus rhombeus**	*N*	*Serrasalmus* sp. 2	*N*	*Pristobrycon striolatus*	*N*
Body length	469 (313–668)	20	367 (294–405)	3		
Greatest width	86 (53–103)	23	88 (79–101)	3		
Pharynx	28 (22–32)	31	25 (23–27)	5		
Haptor length	45 (36–59)	14	38 (36–40)	3		
Haptor width	75 (61–90)	14	77 (71–80)	3		
Hooks 1–7	30 (25–34)	111	29 (25–33)	76	30 (28–31)	5
4A	16 (14–17)	10	15 (14–16)	8	16–17	2
Testis length	115 (55–206)	19	66 (55–77)	2		
Testis width	34 (18–49)	20	34 (25–44)	2		
Ovary length	53 (29–77)	24	40 (34–47)	2		
Ovary width	24 (15–36)	25	26 (19–32)	2		
Cirrus length	60 (51–68)	46	62 (58–72)	16	64 (62–66)	2
Accessory piece	47 (43–52)	40	49 (46–55)	22	52 (48–55)	2

* Type series.

bend of the accessory piece. The specific name is from Greek (skapanē = spade) and refers to the morphology of the cirral base.

Anacanthorus amazonicus sp. n. (Figs. 4, 16–19)

TYPE HOST AND LOCALITIES: *Serrasalmus rhombeus* (Linnaeus), Rio Pitinga, Igarape Agua Branca, Rio Uatumã a tributary of Rio Amazonas, Amazonas, Brazil (15 September 1985) (type); Rio Uatumã, Amazonas, Brazil (collection date unknown); Rio Negro near Manaus, Amazonas, Brazil (28 December 1988).

OTHER RECORDS: *Serrasalmus* sp. (2 of Jégu), from Santa Luzia, Rio Uatumã, Amazonas, Brazil (20 September 1985); Nazare, Rio Uatumã, Amazonas, Brazil (17 September 1985); Rio Pitinga, Igarape Agua Branca, Rio Uatumã, Amazonas, Brazil (15 September 1985). *Pristobrycon striolatus* (Steindachner), from Santa Luzia, Rio Uatumã, Amazonas, Brazil (20 September 1985); Lago Samaumã, Rio Uatumã, Amazonas, Brazil (25 September 1985).

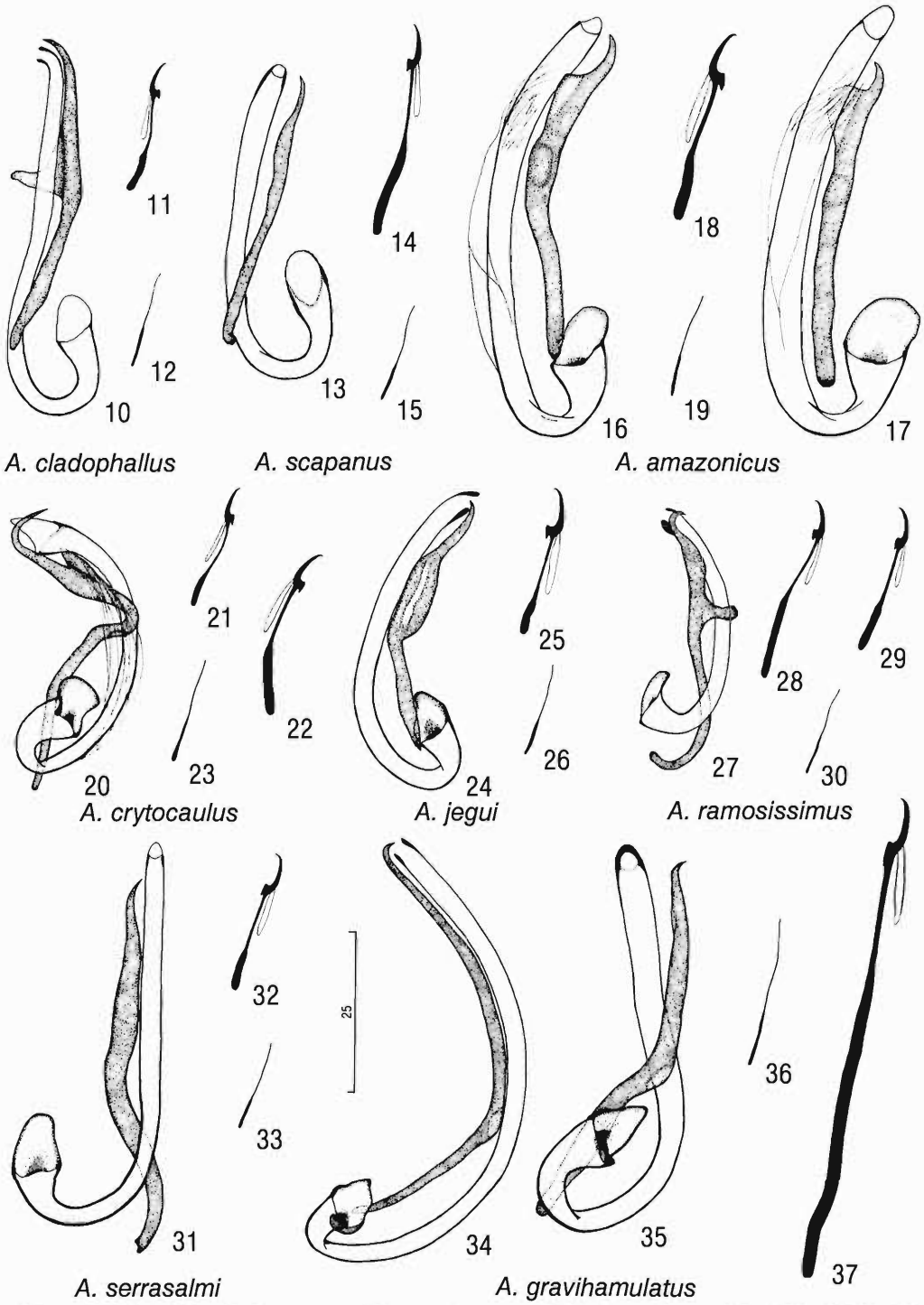
SPECIMENS: Holotype, INPA PA336; paratypes, USNM 81741, 81742, 81743, HWML 33381; vouchers, USNM 81744, 81745, 81746, 81747, 81748.

DESCRIPTION (based on 73 specimens): Body fusiform, greatest width near midlength. Cephalic lobes well developed. Four eyes, equidistant; members of posterior pair larger than those of anterior pair; granules elongate ovate, small; accessory granules occasionally in cephalic region. Pharynx subspherical. Hooks similar; each with slightly depressed thumb, proximal expansion of shank; proximal expansion about 0.5 shank length; FH loop approximately 0.5 shank length. 4A's similar; each expanded about 0.5 length. Gonads slightly overlapping. Cirrus, accessory piece nonarticulating. Cirrus J-shaped, with short basal flap, submedial "feather," slight thickening of terminal shaft wall. Accessory piece rod-shaped, with hooked acute tip, submedial (muscle) articulation point slightly elevated, variable subterminal flap. Comparative measurements provided in Table 1.

REMARKS: *Anacanthorus amazonicus* resembles *A. lepyrophallus* Kritsky, Boeger, and Van Every, 1992, and *A. xaniophallus* Kritsky, Boeger, and Van Every, 1992, in the comparative morphology of the cirrus and hooks. It is easily distinguished from *A. xaniophallus* by having a more robust cirrus and a flap on the distal portion of the accessory piece. *Anacanthorus amazonicus* differs from *A. lepyrophallus* by lacking a subterminal opening of the cirral tip. The specific name refers to the Amazon Basin where the specimens were collected.

Anacanthorus crytocaulus sp. n. (Figs. 5, 20–23)

TYPE HOST AND LOCALITIES: *Pristobrycon striolatus* (Steindachner), Lago Samaumã, Rio Uatumã a tributary of Rio Amazonas, Amazonas, Brazil (25 September 1985) (type); Santa Luzia, Rio Uatumã, Amazonas, Brazil (20 September 1985); Rio Pitinga, Igarape Agua Branca,



Figures 10–37. Sclerotized structures of *Anacanthorus* spp. 10–12. ***Anacanthorus cladophallus.*** **10. Copulatory complex. 11. Hook. 12. 4A. 13–15. *Anacanthorus scapanus.* 13. Copulatory complex. 14. Hook. 15. 4A. 16–19. *Anacanthorus amazonicus.* 16, 17. Copulatory complexes. 18. Hook. 19. 4A. 20–23. *Anacanthorus crytocaulus.* 20. Copulatory complex. 21. Hook pairs 1, 2, 5–7. 22. Hook pairs 3, 4. 23. 4A. 24–26. *Anacanthorus jegui.* 24. Copulatory complex. 25. Hook. 26. 4A. 27–30. *Anacanthorus ramosissimus.* 27. Copulatory complex. 28. Hook**

Rio Uatumã, Amazonas, Brazil (15 September 1985).

TYPE SPECIMENS: Holotype, INPA PA337; paratypes, USNM 81749, 81750, HWML 33382.

DESCRIPTION (based on 110 specimens): Body fusiform, 404 (259–570; $N = 41$) long; greatest width 71 (52–101; $N = 51$) near midlength. Cephalic lobes well developed. Four eyes; members of posterior pair closer together, larger than members of anterior pair; granules elongate ovate, small; accessory granules absent. Pharynx subspherical, 17 (12–23; $N = 49$) in diameter. Haptor 42 (33–53; $N = 43$) long, 79 (59–119; $N = 43$) wide. Hooks similar; each with slightly depressed thumb, shank expanded proximally; hook pairs 3, 4: 29 (26–31; $N = 33$) long, proximal expansion about 0.4 shank length; pairs 1, 2, 5–7: 25 (21–28; $N = 44$) long, proximal expansion about 0.3 shank length; FH loop approximately 0.5 shank length. 4A's similar; each 14 (12–16; $N = 9$) long, proximally expanded about 0.5 length. Gonads slightly overlapping; testis 71 (42–97; $N = 38$) × 23 (13–38; $N = 36$); ovary 46 (29–67; $N = 39$) × 22 (13–28; $N = 40$). Cirrus, accessory piece nonarticulating. Cirrus 42 (34–51; $N = 52$) long, J-shaped, with curved shaft, small basal flap, submedial "feather," flared tip. Accessory piece 47 (39–56; $N = 41$) long, rod-shaped, with moderately raised (muscle) articulation point proximal to submedial loop, subterminal thumb, acute terminal hook.

REMARKS: *Anacanthorus crytocaulus* is sister species to *A. cinctus* sp. n. (Fig. 70). It is easily differentiated from *A. cinctus* by possessing a cirral "feather" and by the absence of a corrugated peduncle. *Anacanthorus crytocaulus* also resembles *A. lasiophallus* sp. n. but is easily differentiated from this species by having an unique median loop of the accessory piece and in the comparative morphology of the proximal expansion of the hook shank. The specific name is from Greek (*cryto* = curved, + *caulis* = stem) and refers to the curvature of the accessory piece.

Anacanthorus jegui sp. n. (Figs. 6, 24–26)

TYPE HOST AND LOCALITIES: *Serrasalmus rhombeus* (Linnaeus), Rio Uatumã, a tributary of Rio Amazonas, Amazonas, Brazil (collection date unknown) (type); Rio Pitinga, Igarape Agua Branca, Rio Uatumã, Amazonas, Brazil (15 September 1985).

TYPE SPECIMENS: Holotype, INPA PA338; paratypes, USNM 81751, HWML 33383.

DESCRIPTION (based on 10 specimens): Body fusiform, 478 (458–503; $N = 4$) long; greatest width 77 (69–91; $N = 5$) along trunk. Cephalic lobes well developed. Four eyes, equidistant; members of posterior pair larger than those of anterior pair; granules small, elongate ovate; accessory granules absent. Pharynx subspherical, 27 (24–30; $N = 5$) in diameter. Haptor 35 (34–36; $N = 2$) long, 69 (52–87; $N = 2$) wide. Hooks similar; each with slightly depressed thumb, shank expanded proximally; hook pairs 3, 4: 25 (24–26; $N = 3$) long, proximal expansion about 0.4 shank length; pairs 1, 2, 5–7: 23 (22–23; $N = 12$) long, proximal expansion about 0.3 shank length; FH loop approximately 0.6 shank length. 4A's similar; each 15 (15–16; $N = 4$) long, proximally expanded about 0.5 length. Gonads slightly overlapping; testis 96 (87–107; $N = 3$) × 31 (29–35; $N = 3$); ovary 48 (36–58; $N = 3$) × 24 (19–33; $N = 3$). Cirrus, accessory piece nonarticulated. Cirrus 48 (45–51; $N = 10$) long, J-shaped, with short basal flap, curved shaft, terminal thickening of shaft wall. Accessory piece 39 (35–42; $N = 9$) long, rod-shaped, with acute termination, submedial (muscle) articulation point indistinct, subterminal expansion originating from both margins of shaft.

REMARKS: *Anacanthorus jegui* resembles *A. serrasalmi* sp. n. in the comparative morphology of the copulatory complex and hooks. *Anacanthorus jegui* differs from this species by having a submedian expansion of the accessory piece that originates from both margins. Morphotypes differing primarily in the extent of the marginal expansions of the accessory piece have been found on several other serrasalmid hosts (compare Fig. 24 to figs. 57–59 in Kritsky et al. 1992). Based on the generally high host specificity exhibited by the Monogenoidea, these forms may comprise a closely related group of species. This species is named for Michel Jégu who collected and identified the majority of hosts for this study.

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pairs 3, 4. 29. Hook pairs 1, 2, 5–7. 30. 4A. 31–33. *Anacanthorus serrasalmi*. 31. Copulatory complex. 32. Hook. 33. 4A. 34–37. *Anacanthorus gravihamulatus*. 34, 35. Copulatory complexes. 36. 4A. 37. Hook. All figures are drawn to the same 25-μm scale.

Anacanthorus ramosissimus sp. n. (Figs. 7, 27–30)

TYPE HOST AND LOCALITY: *Serrasalmus elongatus* Kner, Rio Solimões near Ilha da Marchantaria, Manaus, Amazonas, Brazil (26 November 1984).

TYPE SPECIMENS: Holotype, INPA PA339; paratypes, USNM 81752, HWML 33384.

DESCRIPTION (based on 41 specimens): Body fusiform, 439 (360–545; $N = 16$) long; greatest width 82 (54–104 $N = 23$) along trunk. Cephalic lobes well developed. Four eyes, equidistant; members of posterior pair larger than those of anterior pair; granules elongate ovate, small; accessory granules occasionally scattered in cephalic area. Pharynx spherical, 22 (17–29; $N = 22$) in diameter. Haptor 42 (35–48; $N = 11$) long, 76 (61–84; $N = 11$) wide. Hooks similar; each with slightly depressed thumb, shank expanded proximally; hook pairs 3, 4: 29 (26–32; $N = 18$) long, proximal expansion about 0.6 shank length; pairs 1, 2, 5–7: 26 (23–30; $N = 33$) long, proximal expansion about 0.5 shank length; FH loop approximately 0.4 shank length. 4A's similar; each 13–14 ($N = 5$) long, proximally expanded about 0.5 length. Gonads slightly overlapping; testis 87 (63–114; $N = 15$) × 29 (20–41; $N = 15$); ovary 60 (48–78; $N = 17$) × 29 (20–39; $N = 18$). Cirrus, accessory piece nonarticulated. Cirrus 33 (32–36; $N = 10$) long, approaching J-shaped, with small basal flap, curved shaft, terminal thickening of shaft wall. Accessory piece 36 (33–40; $N = 12$) long, sigmoid, with shaft slightly expanded subterminally, heavy acute terminal hook; submedial (muscle) articulation point modified into a protruding submedian branch.

REMARKS: *Anacanthorus ramosissimus* is sister species to *A. cladophallus* sp. n. (Fig. 70). *Anacanthorus ramosissimus* is easily differentiated from this species by having a sigmoid accessory piece which extends past the proximal portion of the cirrus and by lacking a distinctly J-shaped cirrus. The specific name is from Latin (*ramus* = a branch + *-issimus* = most) and refers to the submedial (muscle) articulation point (branched) on the accessory piece.

Anacanthorus serrasalmi sp. n. (Figs. 8, 31–33)

TYPE HOST AND LOCALITIES: *Serrasalmus rhombeus* (Linnaeus), Rio Pitinga, Igarape Agua Branca, Rio Uatumã a tributary of Rio Amazonas, Amazonas, Brazil (15 September 1985) (type); Rio Uatumã, Amazonas, Brazil (collection date unknown); Rio Negro near Manaus, Amazonas, Brazil (28 December 1988).

OTHER RECORDS: *Serrasalmus elongatus* Kner, from Rio Solimões near Ilha da Marchantaria, Manaus, Amazonas, Brazil (26 November 1984); Rio Negro near Manaus, Amazonas, Brazil (28 December 1988). *Serrasalmus* sp. (2 of Jégu), from Rio Pitinga, Igarape Agua Branca, Rio Uatumã, Amazonas, Brazil (15 September 1985). *Serrasalmus* sp. (2n = 58), from Rio Negro near Manaus, Amazonas, Brazil (5 January 1989). *Pristobrycon* sp., from C. Miriti, Rio Uatumã a tributary of Rio Amazonas, Amazonas, Brazil (26 September 1985).

SPECIMENS: Holotype, INPA PA340; paratypes, USNM 81753, 81754, HWML 33385; vouchers, USNM 81755, 81756, 81757, 81758, 81759.

DESCRIPTION (based on 24 specimens): Body fusiform, greatest width near midlength or in posterior trunk. Cephalic lobes well developed. Four eyes poorly developed, frequently dissociated; members of anterior pair smaller, closer together than those of posterior pair; granules elongate ovate, variable in size; accessory granules in anterior trunk, cephalic region. Pharynx subspherical. Hooks similar; each with slightly depressed thumb, proximal expansion of shank; hook pairs 3, 4 proximal expansion about 0.5 shank length; pairs 1, 2, 5–7 proximal expansion about 0.4 shank length; FH loop approximately 0.5 shank length. 4A's similar; each proximally expanded about 0.5 length. Gonads slightly overlapping. Cirrus, accessory piece nonarticulated. Cirrus J-shaped, with short basal flap, slight terminal thickening of shaft wall. Accessory piece rod-shaped, with moderate angular bend near midlength, indistinct submedial (muscle) articulation point, acute termination. Comparative measurements provided in Table 2.

REMARKS: *Anacanthorus serrasalmi* is similar to *A. scapanus* and *A. gravihamulatus* spp. n. in the comparative morphology of the copulatory complex. *Anacanthorus serrasalmi* is differentiated from *A. scapanus* by possessing a more robust accessory piece with an angular bend near midlength. It is differentiated from *A. gravihamulatus* in the comparative morphology of the hooks. The specific name is derived from the generic name of the host.

Table 2. Comparative measurements (in micrometers; mean with range in parentheses) of *Anacanthorus serrasalmi* from 6 piranha hosts.

	*Serrasalmus rhombeus**	*N*	*Serrasalmus elongatus*	*N*	*Serrasalmus* sp. 2	*N*	*Serrasalmus* sp. 1	*N*	*Serrasalmus* sp. (2n = 58)	*N*	*Pristobrycon* sp.	*N*
Body length	367 (271–445)	11	332	1	319	1	528	1				
Greatest width	70 (54–90)	13	71	1	57	1	105	1				
Pharynx	24 (20–34)	14	21	1	20	1	33	1				
Haptor length	41 (36–48)	8			28	1						
Haptor width	69 (62–85)	7			59	1						
Hooks 3, 4	27 (25–28)	11	27	2	26	1	26–27	3			26–27	3
Hooks 1, 2, 5–7	24 (22–25)	21	24	2			23–24	5			23 (22–24)	3
4A	14 (13–14)	5	13	1			14	1			14	1
Testis length	69 (39–98)	11	58	1	54	1	74	1				
Testis width	25 (16–33)	11	28	1	14	1	40	1				
Ovary length	40 (25–49)	12	32	1	37	1	61	1				
Ovary width	23 (17–31)	12	26	1	16	1	34	1				
Cirrus length	56 (49–64)	22	59–60	2	50	1	62 (59–64)	4	57 (51–63)	2	56–57	2
Accessory piece	52 (48–57)	15	53–54	2	48	1	57 (56–58)	4	47 (42–51)	2	55–56	2

* Type series.

Anacanthorus gravihamulatus sp. n. (Figs. 9, 34–37)

TYPE HOST AND LOCALITIES: *Serrasalmus rhombeus* (Linnaeus), Rio Pitinga, Igarape Agua Branca, Rio Uatumã a tributary of Rio Amazonas, Amazonas, Brazil (15 September 1985) (type); Rio Uatumã, Amazonas, Brazil (collection date unknown).

OTHER RECORDS: *Pristobrycon eigenmanni* (Norman), from Nazare, Rio Uatumã, Amazonas, Brazil (17 September 1985). *Serrasalmus* sp. (2 of Jégu), from Nazare, Rio Uatumã a tributary of Rio Amazonas, Amazonas, Brazil (17 September 1985); Rio Pitinga, Igarape Agua Branca, Rio Uatumã, Amazonas, Brazil (15 September 1985).

SPECIMENS: Holotype, INPA PA341; paratypes, USNM 81760, HWML 33386; vouchers, USNM 81761, 81762, 81763, 81764.

DESCRIPTION (based on 34 specimens): Body fusiform, greatest width near midlength or in anterior half of trunk. Cephalic lobes broad, well developed. Four eyes; members of posterior pair larger, closer together than those of anterior pair; granules elongate ovate, small; accessory granules absent. Pharynx subspherical. Hooks similar; each with flattened thumb, shank expanded proximally; proximal expansion about 0.8 shank length; FH loop approximately 0.2 shank length. 4A's similar; each proximally expanded about 0.4 length. Gonads slightly overlapping. Cirrus, accessory piece nonarticulated. Cirrus J-shaped, with variable spathulate basal flap, terminal wall of shaft thickened. Accessory piece rod-shaped, with moderate angular bend near midlength, acute termination; submedial (muscle) articulation point indistinct. Comparative measurements provided in Table 3.

REMARKS: *Anacanthorus gravihamulatus* is sister species to *A. mastigophallus* Kritsky, Boeger, and Van Every, 1992 (Fig. 70). *Anacanthorus gravihamulatus* is differentiated from this species by (1) possessing a simple J-shaped cirrus with the basal opening directed anteriorly (*A. mastigophallus* has a secondarily derived coiled cirrus with the aperture directed posteriorly) and (2) having significantly longer hooks. *Anacanthorus gravihamulatus* is the only known species of this genus with hooks exceeding 55 μm in length. The specific name is from Latin (*gravis* = burdened with + *hamulatus* = a small hook) and refers to the haptoral hooks.

Anacanthorus sciponophallus sp. n. (Figs. 38, 43–54)

TYPE HOST AND LOCALITIES: *Serrasalmus elongatus* Kner, Rio Solimões near Ilha da Marchantaria, Manaus, Amazonas, Brazil (26 November 1984) (type); Rio Negro near Manaus, Amazonas, Brazil (28 December 1988).

OTHER RECORDS: *Serrasalmus rhombeus* (Linnaeus), from Rio Pitinga, Igarape Agua Branca, Rio Uatumã, Amazonas, Brazil (15 Sep-

Table 3. Comparative measurements (in micrometers; mean with range in parentheses) of *Anacanthorus gravihamulatus* from 3 piranha hosts.

	*Serrasalmus rhombeus**	*N*	Serrasalmus sp. 2	*N*	*Pristobrycon eigenmanni*	*N*
Body length	549 (342–716)	13	538	1	521 (466–578)	2
Greatest width	95 (77–125)	18	112	1	103	1
Pharynx	36 (29–42)	16	32	1	37 (36–38)	2
Haptor length	90 (69–105)	12	87	1	63	1
Haptor width	61 (52–70)	12	73	1	69	1
Hooks 1–7	70 (56–78)	41	63 (61–65)	14	63 (58–70)	6
4A	22 (21–23)	5	21	1	23	1
Testis length	107 (65–211)	9	110	1	55	1
Testis width	33 (19–44)	9	45	1	12	1
Ovary length	57 (36–87)	14	50	1	84 (79–89)	2
Ovary width	28 (23–39)	14	30	1	32–33	2
Cirrus length	63 (56–71)	9	59 (53–66)	4	43 (42–44)	2
Accessory piece	59 (55–65)	7	58 (52–61)	3	40	1

* Type series.

tember 1985); Rio Negro near Manaus, Amazonas, Brazil (28 December 1988). *Serrasalmus spilopleura* Kner, from Rio Solimões near Ilha da Marchantaria, Manaus, Amazonas, Brazil (14 September 1984, 26 November 1984). *Serrasalmus* sp. (1 of Jégu), from Rio Solimões near Ilha da Marchantaria, Manaus, Amazonas, Brazil (26 November 1984). *Serrasalmus* sp. (2 of Jégu), from Nazare, Rio Uatumã, Amazonas, Brazil (17 September 1985). *Serrasalmus* sp. (2n = 58), from Lago do Rei, Paraná, Ilha do Careiro, Amazonas, Brazil (28 February 1986); Rio Negro near Manaus, Amazonas, Brazil (28 December 1988).

SPECIMENS: Holotype, INPA PA342; paratypes, USNM 81765, HWML 33387; vouchers, USNM 81766, 81767, 81768, 81769, 81770, 81771, 81796.

DESCRIPTION (based on 27 specimens): Body fusiform, greatest width near midlength. Cephalic lobes well developed. Four eyes; members of posterior pair larger, farther apart than those of anterior pair; granules elongate ovate, variable in size; accessory granules absent. Hooks similar; each with slightly depressed thumb, shank expanded proximally; proximal expansion of hook pairs 3, 4 about 0.5 shank length; pairs 1, 2, 5–7 proximal expansion about 0.4 shank length; FH loop approximately 0.5 shank length. 4A's similar; each proximally expanded about 0.5 length. Gonads slightly overlapping. Cirrus, accessory piece nonarticulated. Cirrus J-shaped, basal flap small ovate, shaft wall terminally thickened. Accessory piece rod-shaped, with acute slightly recurved tip; submedial (muscle) articulation point indistinct to slightly elevated. Comparative measurements provided in Table 4.

REMARKS: *Anacanthorus sciponophallus* resembles *A. serrasalmi* sp. n. in the comparative morphology of the copulatory complex and the hooks. *Anacanthorus sciponophallus* is most easily differentiated from this species by having a smaller, more ovate cirral base and a long straight accessory piece with a slightly recurved tip. Several morphotypes (Figs. 43, 47, 51) of this species were found which differ in the morphology of the cirral base and accessory piece. These forms, apparently restricted to specific hosts, may comprise a closely related complex of species. The specific name is from Greek (*skipōnos* = a staff + *phallos* = penis) and refers to the morphology of the copulatory complex.

Anacanthorus mesocondylus sp. n. (Figs. 39, 55–58)

TYPE HOST AND LOCALITIES: *Serrasalmus elongatus* Kner, Rio Solimões near Ilha da Marchantaria, Manaus, Amazonas, Brazil (26 November 1984) (type); Rio Negro near Manaus, Amazonas, Brazil (28 December 1988).

OTHER RECORDS: *Pristobrycon eigenmanni* (Norman), from Santa Luzia, Rio Uatumã, Amazonas, Brazil (20 September 1985); Rio Negro near Manaus, Amazonas, Brazil (28 December 1988). *Pristobrycon* sp., from C. Miriti, Rio Uatumã, Amazonas, Brazil (26 September 1985). *Serrasalmus rhombeus* (Linnaeus), Rio Uatumã, Amazonas, Brazil (collection date unknown); Rio

Pitinga, Igarape Agua Branca, Rio Uatumã, Amazonas, Brazil (15 September 1985); Rio Negro near Manaus, Amazonas, Brazil (28 December 1988). *Serrasalmus spilopleura* Kner, Rio Solimões near Ilha da Marchantaria, Manaus, Amazonas, Brazil (26 November 1984). *Serrasalmus* sp. (1 of Jégu), Rio Solimões near Ilha da Marchantaria, Manaus, Amazonas, Brazil (26 November 1984). *Serrasalmus* sp. (2 of Jégu), from Santa Luzia, Rio Uatumã, Amazonas, Brazil (20 September 1985); Rio Pitinga, Igarape Agua Branca, Rio Uatumã, Amazonas, Brazil (15 September 1985); Nazare, Rio Uatumã, Amazonas, Brazil (17 September 1985).

SPECIMENS: Holotype, INPA PA343; paratypes, USNM 81772, HWML 33388; vouchers, USNM 81773, 81774, 81775, 81776, 81777, 81778, 81779, 81780, 81781, 81782, 81783, 81784, 81785.

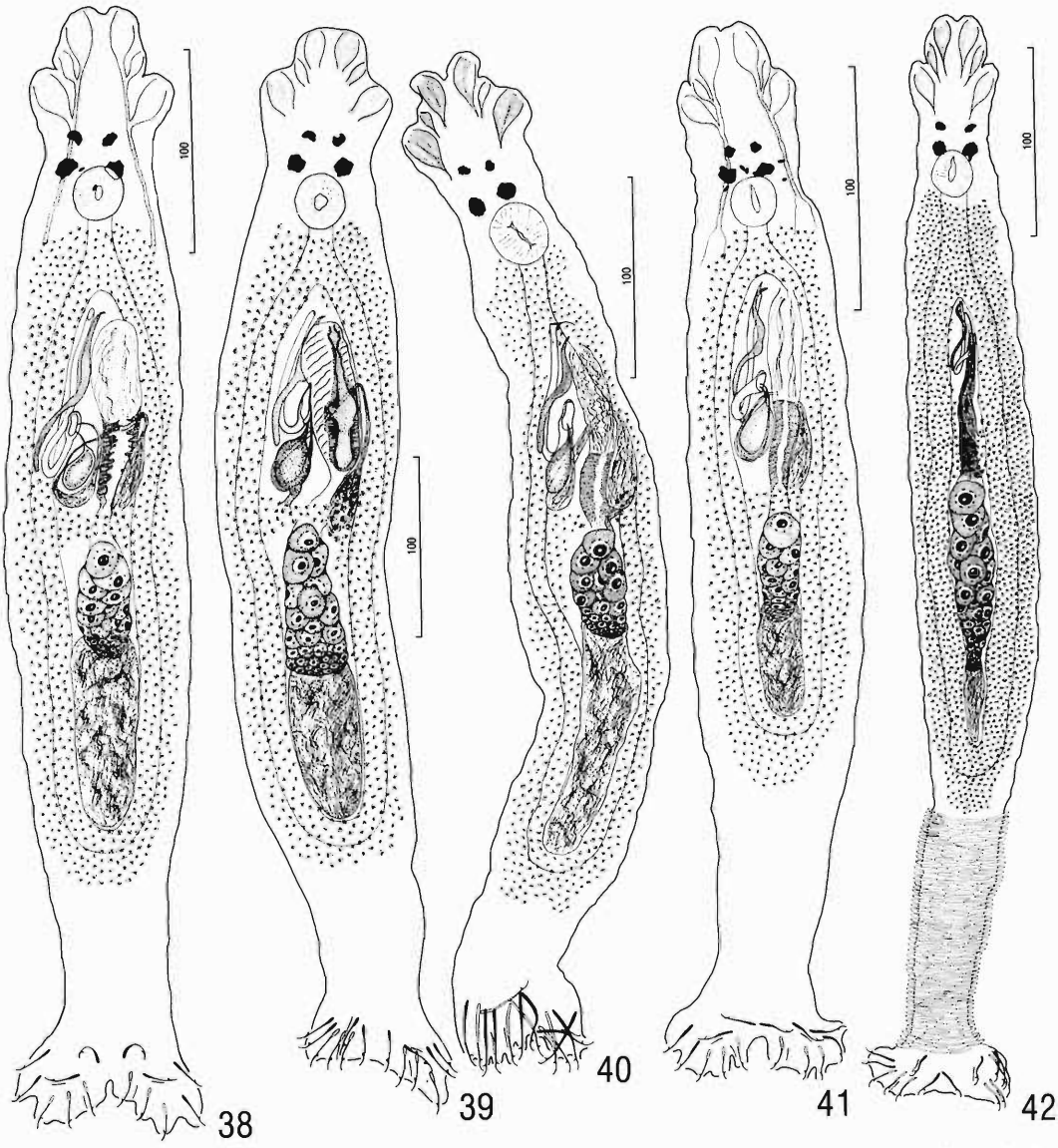
DESCRIPTION (based on 23 specimens): Body fusiform, greatest width near midlength or in anterior half. Cephalic lobes well developed. Four eyes; members of posterior pair larger, farther apart than those of anterior pair; granules elongate ovate, small; accessory granules absent. Pharynx subspherical. Hooks similar; each with depressed thumb, proximal expansion of shank; hook pairs 3, 4 proximal expansion about 0.5 shank length; pairs 1, 2, 5–7 proximal expansion about 0.4 shank length; FH loop approximately 0.5 shank length. 4A's similar; each proximally expanded about 0.5 length. Gonads slightly overlapping. Cirrus, accessory piece nonarticulated. Cirrus broadly J-shaped, with elongate basal flap extending to proximal apex, slight terminal thickening of shaft wall. Accessory piece rod-shaped, with acute slightly recurved termination; submedial (muscle) articulation point a raised, rounded knob. Comparative measurements provided in Table 5.

REMARKS: *Anacanthorus mesocondylus* is sister species to *A. cladophallus* sp. n., *A. ramosissimus* sp. n., and *A. reginae* Boeger and Kritsky, 1988 (Fig. 70). *Anacanthorus mesocondylus* is easily differentiated from these species by having an elongate, pointed flap on the cirral base, and a conspicuous rounded medial knob on the accessory piece. This species was found on numerous hosts; no significant morphological or size differences were observed among the populations. The specific name is from Greek (*mesos* = middle + *kondylos* = knob) and refers to the submedial (muscle) articulation point of the accessory piece.

Table 4. Comparative measurements (in micrometers; mean with range in parentheses) of *Anacanthorus sciponophallus* from 6 piranha hosts.

	*Serrasalmus elongatus**	N	*Serrasalmus spilopleura*	N	*Serrasalmus rhombeus*	N	*Serrasalmus* sp. 1	N	*Serrasalmus* sp. 2	N	*Serrasalmus* sp. (2n = 58)	N
Body length	431 (287–556)	17	426 (356–481)	15	376 (374–379)	2	384 (332–486)	7	260	1		
Greatest width	78 (59–94)	17	106 (80–133)	15	73 (60–84)	5	84 (62–94)	8	86	1		
Pharynx	25 (21–29)	18	34 (29–36)	14	29 (22–33)	3	25 (21–27)	7	24	1	25	1
Haptor length	38 (26–55)	11	41 (32–49)	14	33	1	36 (31–42)	5				
Haptor width	82 (63–117)	11	86 (70–109)	13	66	1	72 (66–79)	5				
Hooks 3, 4	22 (20–24)	6	23 (22–25)	6	25	4	23 (22–24)	9	21 (19–23)	2	24 (23–26)	9
Hooks 1, 2, 5–7	19 (17–20)	10	20 (19–22)	6	22 (21–23)	6	20 (19–22)	16			20 (19–21)	11
4A	12–13	3	12	1	12–13	2	13	6			12–13	3
Testis length	65 (50–87)	10	73 (52–83)	11	52	1	20	1				
Testis width	27 (23–31)	10	38 (28–59)	11	28 (23–33)	2						
Ovary length	50 (38–62)	12	49 (42–55)	12	39	1						
Ovary width	28 (19–38)	11	36 (27–50)	12	16	1	27 (25–29)	2				
Cirrus length	79 (69–91)	26	76 (68–87)	18	82 (74–95)	7	79 (72–87)	17	79 (76–82)	3	81 (72–92)	16
Accessory piece	76 (65–83)	24	74 (65–78)	18	79 (73–85)	7	76 (68–83)	17	76 (74–77)	2	76 (69–84)	15

* Type series.



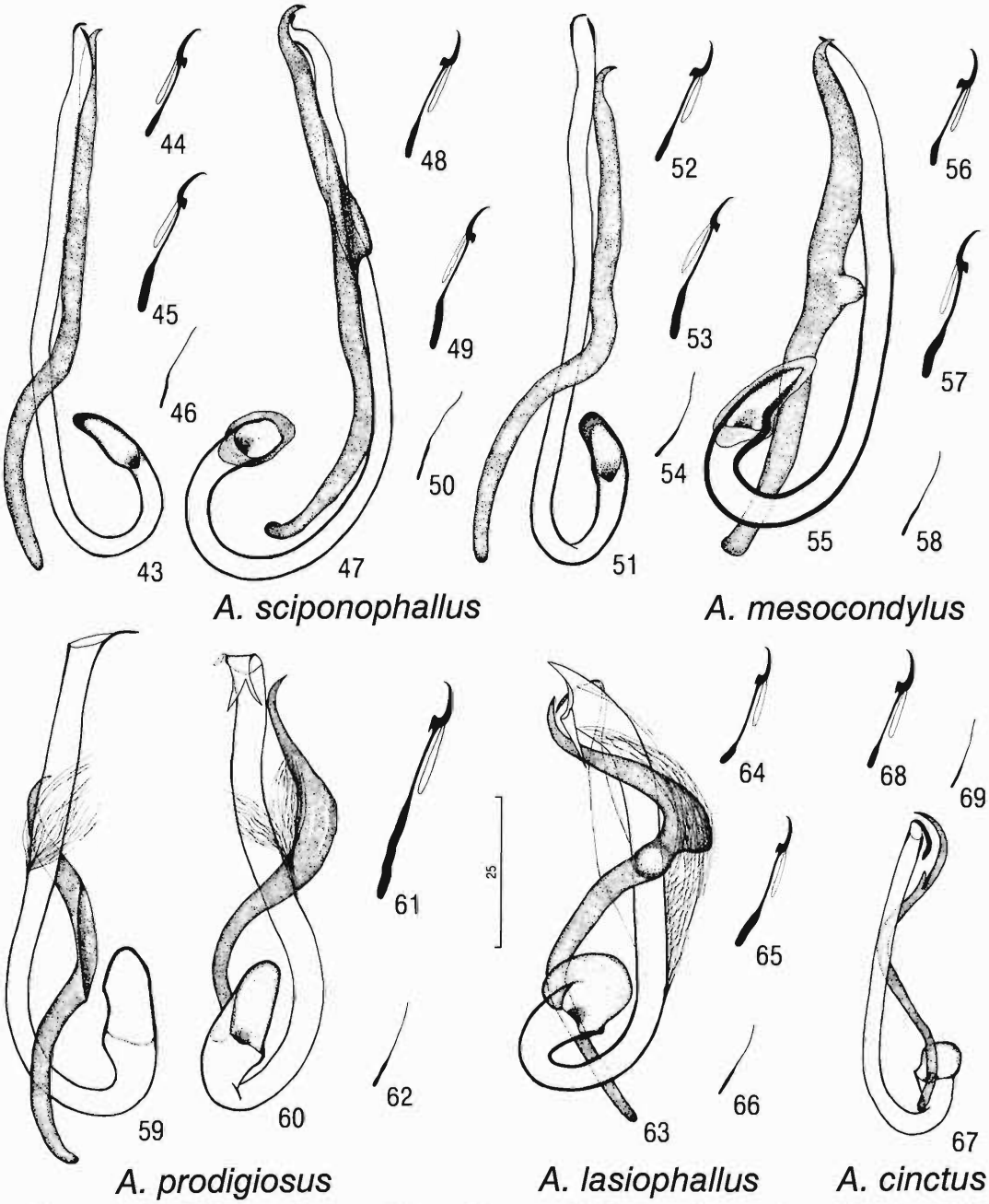
Figures 38–42. Whole mount illustrations (ventral) of *Anacanthorus* spp. 38. *Anacanthorus sciponophallus* (holotype). 39. *Anacanthorus mesocondylus* (holotype). 40. *Anacanthorus prodigiosus* (holotype). 41. *Anacanthorus lasiophallus* (holotype). 42. *Anacanthorus cinctus* (holotype).

Anacanthorus prodigiosus sp. n. (Figs. 40, 59–62)

TYPE HOST AND LOCALITY: *Serrasalmus elongatus* Kner, Rio Negro near Manaus, Amazonas, Brazil (28 December 1988).

OTHER RECORDS: *Serrasalmus rhombeus* (Linnaeus), from Rio Uatumã, Amazonas, Brazil (collection date unknown); Rio Pitinga, Igarape Agua Branca, Rio Uatumã, Amazonas, Brazil (15 September 1985); Rio Negro near Manaus, Amazonas, Brazil (28 December 1988). *Serrasalmus* sp. (1 of Jégu), Rio Solimões near Ilha da Marchantaria, Manaus, Amazonas, Brazil (26 November 1984). *Serrasalmus* sp. (2 of Jégu), Nazare, Rio Uatumã, Amazonas, Brazil (17 September 1985); Rio Pitinga, Igarape Agua Branca, Rio Uatumã, Amazonas, Brazil (15 September 1985).

SPECIMENS: Holotype, INPA PA344; paratypes, USNM 81786, HWML 33389; vouchers



Figures 43–69. Sclerotized structures of *Anacanthorus* spp. 43–54. *Anacanthorus sciponophallus* from 3 different hosts. 43–46. *A. sciponophallus* from *Serrasalmus elongatus*. 43. Copulatory complex. 44. Hook pairs 1, 2, 5–7. 45. Hook pairs 3, 4. 46. 4A. 47–50. *A. sciponophallus* from *S. rhombeus*. 47. Copulatory complex. 48. Hook pairs 1, 2, 5–7. 49. Hook pairs 3, 4. 50. 4A. 51–54. *A. sciponophallus* from *S. spilopleura*. 51. Copulatory complex. 52. Hook pairs 1, 2, 5–7. 53. Hook pairs 3, 4. 54. 4A. 55–58. *Anacanthorus mesocondylus*. 55. Copulatory complex. 56. Hook pairs 1, 2, 5–7. 57. Hook pairs 3, 4. 58. 4A. 59–62. *Anacanthorus prodigiosus*. 59, 60. Copulatory complexes. 61. Hook. 62. 4A. 63–66. *Anacanthorus lasiophallus*. 63. Copulatory complex. 64. Hook pairs 1, 2, 5–7. 65. Hook pairs 3, 4. 66. 4A. 67–69. *Anacanthorus cinctus*. 67. Copulatory complex. 68. Hook. 69. 4A. All figures are drawn to the same 25-μm scale.

Table 5. Comparative measurements (in micrometers; mean with range in parentheses) of ***Anacanthorus mesocondylus*** from 7 piranha hosts.

	*Serrasalmus elongatus**	*N*	*Serrasalmus rhombeus*	*N*	*Serrasalmus spilopleura*	*N*	*Serrasalmus* sp. 1	*N*	*Serrasalmus* sp. 2	*N*	*Pristobrycon* sp.	*N*	*Pristobrycon eigenmanni*	*N*
Body length	457 (316–601)	9	410 (336–535)	8			418 (363–491)	4	359 (320–398)	2	386 (321–418)	4	358 (302–414)	2
Greatest width	84 (66–107)	10	81 (64–97)	8			100 (95–112)	4	74 (58–89)	2	79 (59–94)	6	75 (73–78)	2
Pharynx	26 (22–31)	12	27 (22–29)	6			28 (26–31)	4	25 (23–28)	2	26 (22–30)	5	25 (23–27)	2
Haptor length	39 (29–47)	9	41 (34–48)	5			41 (38–43)	4	39 (38–40)	2	35 (34–36)	4	38 (36–41)	2
Haptor width	77 (59–94)	9	75 (65–80)	5			79 (71–92)	4	69 (62–76)	2	69 (62–80)	4	84 (80–88)	2
Hooks 3, 4	23 (21–24)	8	23–24	6	24–25	2	23	2	23 (20–25)	7	23 (22–25)	13	23 (21–26)	12
Hooks 1, 2, 5–7	20 (18–21)	17	19 (18–21)	17			19 (18–20)	4	20 (19–25)	14	19 (18–21)	29	19 (18–22)	32
4A	11 (11–12)	3	13 (12–14)	4			12–13	2	11–12	3	13 (12–14)	6	13 (12–14)	7
Testis length	171 (95–208)	9	73 (47–114)	3			72	1	48 (33–62)	3	75 (64–86)	2	44	1
Testis width	71 (50–104)	9	24 (19–31)	3			39	1	22 (19–27)	3	33 (29–38)	2	32	1
Ovary length	58 (31–78)	9	55 (46–65)	2			50 (49–51)	2	43 (36–57)	3	57	1	31	1
Ovary width	29 (20–38)	9	19 (18–20)	2			30 (28–31)	2	22 (13–26)	3	26	1	25	1
Cirrus length	72 (67–76)	22	74 (67–80)	15	85	1	74 (70–82)	6	78 (69–86)	13	77 (72–85)	16	77 (68–84)	11
Accessory piece	74 (61–81)	20	77 (72–80)	15	81	1	76 (72–82)	6	80 (72–86)	13	78 (72–83)	16	79 (69–84)	11

* Type series.

USNM 81787, 81788, 81789, 81790, 81791, 81792.

Description (based on 27 specimens): Body fusiform, greatest width near midlength. Cephalic lobes well developed. Four eyes, equidistant; members of posterior pair larger than those of anterior pair; granules elongate ovate, small; accessory granules absent. Pharynx spherical. Hooks similar; each with slightly depressed thumb, shank expanded proximally; proximal expansion about 0.6 shank length; FH loop approximately 0.5 shank length. 4A's similar; each proximally expanded about 0.5 length. Gonads slightly overlapping. Cirrus, accessory piece nonarticulated. Cirrus J-shaped, robust, with elongate rounded basal flap, cirral "feather" originating near midlength, terminal bipartite flap at tip of shaft. Accessory piece rod-shaped, with acute tip, broad flaplike expansion along distal half; submedial (muscle) articulation point indistinct. Comparative measurements provided in Table 6.

Remarks: *Anacanthorus prodigiosus* is similar to *A. lepyrophallus* Kritsky, Boeger, and Van Every, 1992, and *A. lasiophallus* sp. n. in the comparative morphology of the copulatory complex. It is easily differentiated from *A. lepyrophallus* by having a broad subterminal expansion of the accessory piece and an extended bipartite flap on the distal end of the cirrus. *Anacanthorus prodigiosus* differs from *A. lasiophallus* by lacking a distinct modification of the submedial (muscle) articulation point. Further the hooks of *A. prodigiosus* have a proximal expansion nearly ⅔ of the shank length (hooks of *A. lepyrophallus* and *A. lasiophallus* have a basal expansion of ½ or less). The specific name is from Latin (*prodigiosus* = full of wonder).

Anacanthorus lasiophallus sp. n.
(Figs. 41, 63–66)

Type host and localities: *Pristobrycon striolatus* (Steindachner), Rio Pitinga, Igarape Agua Branca, Rio Uatumã, Amazonas, Brazil (15 September 1985) (type); Santa Luzia, Rio Uatumã, Amazonas, Brazil (20 September 1985); Lago Samaumã, Rio Uatumã, Amazonas, Brazil (25 September 1985).

Type specimens: Holotype, INPA PA345; paratypes, USNM 81793, 81794, HWML 33390.

Description (based on 71 specimens): Body fusiform, 379 (212–551; $N = 25$) long; greatest width 77 (51–102; $N = 28$) near midlength. Ce-

Table 6. Comparative measurements (in micrometers; mean with range in parentheses) of *Anacanthorus prodigiosus* from 4 piranha hosts.

	*Serrasalmus elongatus**	*N*	*Serrasalmus rhombeus*	*N*	*Serrasalmus* sp. 1	*N*	*Serrasalmus* sp. 2	*N*
Body length	438 (377–510)	14	481 (420–626)	5	470 (441-526)	3		
Greatest width	78 (66–91)	16	84 (72–94)	4	106 (90–127)	3		
Pharynx	31 (27–34)	16	29 (26–31)	4	34–35	3		
Haptor length	42 (35–49)	9	56	1	48 (45–50)	2		
Haptor width	71 (59–82)	8	96	1	87 (80–94)	2		
Hooks 1–7	36 (31–40)	40	39 (34–42)	19	36 (33–38)	5	40–41	3
4A	15 (14–16)	7	15–16	3	14	1	16	1
Testis length	82 (67–103)	8	99	1	94	1		
Testis width	24 (14–31)	8	28	1	35	1		
Ovary length	47 (33–59)	12	50	1	61	1		
Ovary width	29 (23–36)	12	26 (24–28)	3	39	1		
Cirrus length	74 (67–78)	24	71 (68–76)	10	68 (67–70)	5	65 (60–69)	2
Accessory piece	60 (55–67)	25	61 (56–65)	9	57 (55–60)	5	53 (50–57)	2

* Type series.

phalic lobes well developed. Four eyes, equidistant; members of posterior pair larger than those of anterior pair; granules elongate ovate, variable in size; accessory granules occasionally scattered in pharyngeal area. Pharynx subspherical, 17 (13–20; $N = 34$) in diameter. Haptor 37 (27–49; $N = 23$) long, 78 (62–92; $N = 23$) wide. Hooks similar; each with slightly depressed thumb, shank expanded proximally; hook pairs 3, 4: 22 (20–23; $N = 43$) long, proximal expansion 0.4 shank length; pairs 1, 2, 5–7: 18 (16–20; $N = 62$) long, proximal expansion about 0.25 shank length; FH loop approximately 0.5 shank length. 4A's similar; each 11 (10–12; $N = 11$) long, proximally expanded about 0.5 length. Gonads slightly overlapping; testis 50 (28–86; $N = 22$) × 25 (18–41; $N = 21$); ovary 42 (18–59; $N = 23$) × 23 (14–35; $N = 22$). Cirrus, accessory piece nonarticulating. Cirrus 65 (54–73; $N = 48$) long, J-shaped, with rounded basal flap, submedial "feather," curved shaft terminally flared, subterminal opening. Accessory piece 64 (53–73; $N = 48$) long, rod-shaped, with acute terminal hook, broad flap extending from subterminal bend; submedial (muscle) articulation point rounded, protruding.

REMARKS: *Anacanthorus lasiophallus* is sister species to *A. crytocaulus* and *A. cinctus* spp. n. (Fig. 70). All 3 species exclusively parasitize *Pristobrycon striolatus* (Fig. 1). *Anacanthorus lasiophallus* is differentiated from *A. crytocaulus* by having a more robust accessory piece with a broad flap on the subterminal bend. It is differentiated from *A. cinctus* by having a cirral "feather" and a distinct modification of the submedial (muscle) articulation point of the accessory piece. The species name is from Greek (*lasios* = hairy + *phallos* = penis) and refers to the cirral "feather."

Anacanthorus cinctus sp. n. (Figs. 42, 67–69)

TYPE HOST AND LOCALITIES: *Pristobrycon striolatus* (Steindachner), Lago Samaumã, Rio Uatumã, Amazonas, Brazil (25 September 1985) (type); Santa Luzia, Rio Uatumã, Amazonas, Brazil (20 September 1985).

TYPE SPECIMENS: Holotype, INPA PA346; paratypes, USNM 81795, HWML 33391.

DESCRIPTION (based on 24 specimens): Body fusiform, 455 (308–579; $N = 11$) long; greatest width 82 (73–90; $N = 7$) near midlength. Cephalic lobes well developed. Four eyes, equidistant; members of posterior pair larger than those of anterior pair; granules elongate ovate, variable in size; accessory granules absent. Pharynx spherical, 21 (18–25; $N = 9$) in diameter. Peduncle elongate, surface corrugated. Haptor 31 (27–36; $N = 7$) long, 72 (64–84; $N = 7$) wide. Hooks similar; each with slightly depressed thumb, shank expanded proximally; hook pairs 3, 4: 21 (20–23; $N = 11$) long, proximal expansion about 0.4 shank length; pairs 1, 2, 5–7: 19 (17–20; $N = 20$) long, proximal expansion about 0.25 shank length; FH loop approximately 0.6 shank length. 4A's similar; each 10–11 ($N = 3$) long, proximally expanded about 0.5 length. Gonads slightly overlapping; testis 32 (30–34; $N = 4$) × 11 (9–12; $N = 3$); ovary 68 (42–99; $N = 8$) × 25 (19–30; $N = 7$). Cirrus, accessory piece

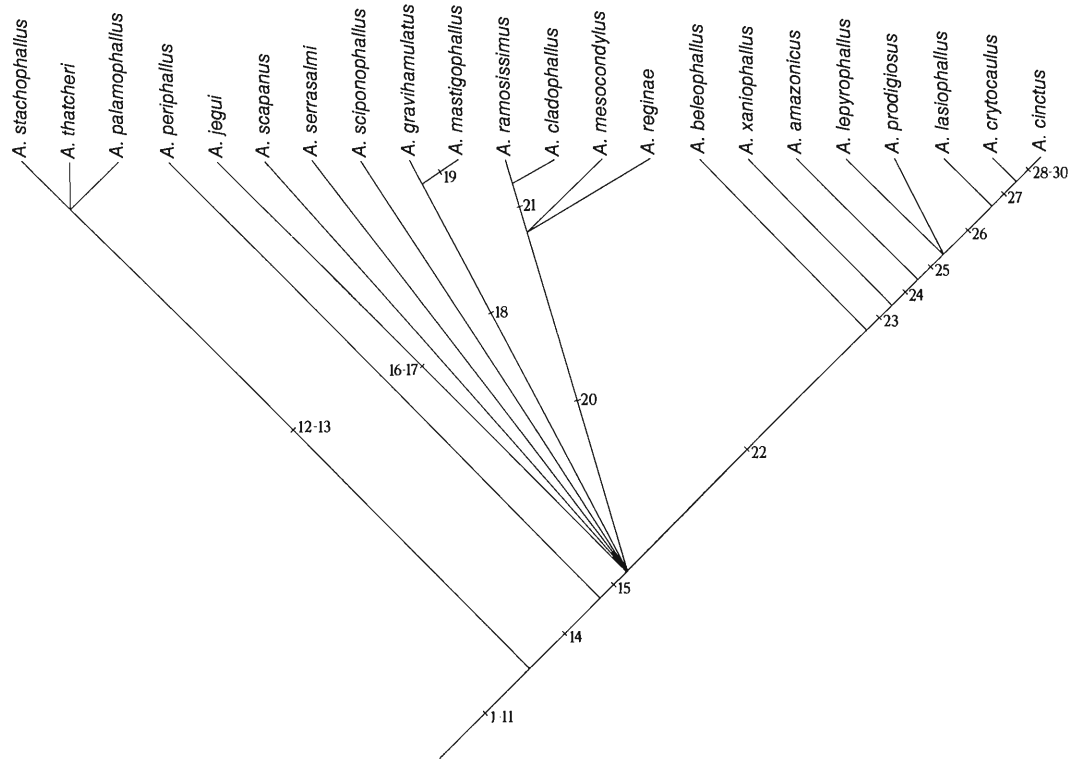


Figure 70. Cladogram depicting evolutionary relationships of *Anacanthorus* species parasitizing 10 species of piranha (Serrasalmidae) from the central Amazon. Numbered slashes refer to postulated evolutionary changes in character states as indicated in the character analysis.

nonarticulated. Cirrus 48 (45–52; $N = 12$) long, J-shaped, with small basal flap, slightly curved shaft, terminally thickened wall, subterminal opening. Accessory piece 45 (40–52; $N = 10$) long, rod-shaped, with moderate curvature near midlength, small subterminal thumb, acute terminal hook; submedial (muscle) articulation point indistinct.

REMARKS: *Anacanthorus cinctus* is sister species to *A. crytocaulus* sp. n. (Fig. 70). *Anacanthorus cinctus* differs from this species by lacking a distinct subterminal loop of the accessory piece and by the absence of a cirral "feather." The cladogram (Fig. 70) suggests that *Anacanthorus cinctus* secondarily lost the cirral "feather" but has retained the derived morphology of the cirral tip and the subterminal thumb of the accessory piece. The corrugated peduncle is an autapomorphy for *A. cinctus*. Further, *A. cinctus* differs from other species of *Anacanthorus* in having an ovarian length nearly twice that of the testis. The specific name is from Latin (*cinctus* = girdled) referring to the tegumental surface of the peduncle.

Phylogenetic Analysis

CHARACTER ANALYSIS: Homologous series utilized in the analysis of parasite phylogeny are listed below. Bold numbers in parentheses indicate the location of postulated character-state changes on the cladogram (Fig. 70); the character-state matrix for the species of *Anacanthorus* is presented in Table 7. Polarity is determined by out-group comparison unless stated otherwise.

1. *Articulation of accessory piece to cirral base.* Plesiomorphy: present. Apomorphy: absent (**1**). The apomorphic state is a synapomorphy for the ingroup.

2. *Shape of cirrus.* Plesiomorphy: straight or with tendency for twisting. Apomorphy: tendency for curling (**2**). Both plesiomorphic and apomorphic states may incorporate forms with coiled cirri. However, differentiation of each state depends on means by which the coil is derived. A coil developed from twisting of the cirrus does not require change in the relative position of the cirral base and/or terminal aperture, while 1

Table 7. Matrix of characters for central Amazonian species of *Anacanthorus* parasitizing 10 species of piranha. Sequence of characters corresponds to listing in character analysis. Homologous series 3 and 9 were unordered in the analysis.

A. amazonicus	1	1	2	1	1	0	0	1	0	0	0	0
A. beleophallus	1	1	1	1	1	0	0	0	9	0	0	0
A. cinctus	1	1	0	1	0	0	0	1	1	0	1	0
A. cladophallus	1	1	0	1	1	0	2	0	9	0	0	0
A. crytocaulus	1	1	2	1	0	0	1	1	1	0	0	0
A. gravihamulatus	1	1	0	1	1	0	0	0	9	0	0	1
A. jegui	1	1	0	1	1	0	0	1	2	0	0	0
A. lasiophallus	1	1	2	1	0	0	1	1	0	0	0	0
A. lepyrophallus	1	1	2	1	0	0	0	1	0	0	0	0
A. mastigophallus	1	1	0	2	1	0	0	0	9	0	0	1
A. mesocondylus	1	1	0	1	1	0	1	0	9	0	0	0
A. palamophallus	1	1	0	0	0	1	0	0	9	1	0	0
A. periphallus	1	1	0	1	0	0	0	0	9	0	0	0
A. prodigiosus	1	1	2	1	0	0	0	1	0	0	0	0
A. ramosissimus	1	1	0	1	1	0	2	0	9	0	0	0
A. reginae	1	1	0	1	1	0	1	0	9	0	0	0
A. scapanus	1	1	0	1	1	0	0	0	9	0	0	0
A. sciponophallus	1	1	0	1	1	0	0	0	9	0	0	0
A. serrasalmi	1	1	0	1	1	0	0	0	9	0	0	0
A. stachophallus	1	1	0	0	0	1	0	0	9	1	0	0
A. thatcheri	1	1	0	0	0	1	0	0	9	1	0	0
A. xaniophallus	1	1	2	1	1	0	0	0	9	0	0	0
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0

formed by curling implies a changed position of either end of the cirrus in relation to the cirral shaft. Cirral shafts developed through twisting are demonstrated in cirri of *Anacanthorus* species infesting *Triportheus* (see Kritsky et al., 1992) and *Salminus* species (see Kritsky and Thatcher, 1974); cirral shafts developed through curling apparently represent a synapomorphy for the *Anacanthorus* ingroup infesting *Pygocentrus, Pristobrycon,* and *Serrasalmus.* In the latter, the coiled cirrus of *A. mastigophallus* Kritsky, Boeger, and Van Every, 1992, appears to be secondarily derived from the J-shaped cirrus of its ancestor (Fig. 70), which in turn has developed from a relatively straight tube (see cirrus of *A. stachophallus* Kritsky, Boeger, and Van Every, 1992 [fig. 105 in Kritsky et al., 1992]).

3. *Cirral "feather."* Plesiomorphy: absent (**3, 28**). Apomorphies: moderately developed, terminal filaments absent (fig. 10 in Kritsky et al., 1992) (**22**); well developed, terminal filaments present (Fig. 63) (**23**).

4. *Basal aperture of cirrus.* Plesiomorphy: aperture opening posterolaterally or laterally (figs. 72, 105 in Kritsky et al., 1992) (**4**). Apomorphies: aperture opening anteriorly or anterolaterally, cirrus J-shaped (Fig. 10) (**14**); aperture opening posteriorly, cirrus curled to form 1 or more rings (fig. 66 in Kritsky et al., 1992) (**19**).

5. *Distal aperture of cirrus.* Plesiomorphy: subterminal (Figs. 20, 60, 63) (**5, 25**). Apomorphy: terminal or diagonal (Figs. 24, 35) (**15**).

6. *Cirral base.* Plesiomorphy: heellike projection absent (Figs. 10, 13) (**6**). Apomorphy: heellike projection present (fig. 105 in Kritsky et al., 1992; figs. 6–8, 23 in Boeger and Kritsky, 1988) (**12**).

7. *Submedial (muscle) articulation point of accessory piece.* Plesiomorphy: flat or minimally elevated (Figs. 17, 31) (**7, 29**). Apomorphies: small protuberance (Figs. 55, 63) (**20, 26**); protruding branch (Figs. 10, 27) (**21**). The submedial (muscle) articulation appears as a roughened area near the midlength of the accessory piece. In contrast, the subterminal expansion (character 8) has a smooth margin.

8. *Subterminal expansion of accessory piece.* Plesiomorphy: absent (Fig. 31) (**8**). Apomorphy: present (Figs. 17, 20, 24) (**16, 24**).

9. *Shape of subterminal expansion of accessory piece* (when present). Plesiomorphy: flaplike, originating from single margin (Figs. 16, 63). Apomorphies: thumblike, from single margin (Figs. 20, 67) (**27**); expanded from both margins (Fig. 24) (**17**). Species lacking a subterminal expansion (see character 8) receive a "9" in the matrix code. Polarity determined by functional outgroup comparison.

10. *Distal tip of accessory piece.* Plesiomorphy: acute (Figs. 20, 31) (**9**). Apomorphy: blunt (figs. 72, 105 in Kritsky et al., 1992) (**13**).

11. *Peduncle surface.* Plesiomorphy: smooth (**10**). Apomorphy: corrugated (Fig. 42) (**30**).

12. *Morphology of thumb on haptoral hooks.*

Plesiomorphy: slightly depressed (Figs. 11, 14, 18) (**11**). Apomorphy: flattened (Fig. 37) (**18**).

Our hypothesis on the phylogenetic relationships of the parasites is based primarily on characters of the copulatory complex. The internal anatomy of *Anacanthorus* species is redundant and, therefore, provides no evolutionary information for the present analysis. Similarly, with the exception of the morphology of the hook thumb, features of the haptor were of limited value for phylogenetic reconstruction.

Since length of the proximal expansion of the hook shank varies both inter- and intraspecifically, ratios between length of the basal expansion and the total shank length were compared across the same hook pair among species (i.e., 1-1, 2-2, etc. [7 possible homologous series]) and also pairwise within a species (i.e., 1-2, 1-3, 2-3 etc. [21 possible series]). This analysis resulted in numerous instances of homoplasy in evolution of the haptor that tended to outweigh effects of all other characters in the analysis. In effect, use of these hook characters masked pertinent information of the other 12 homologous series biasing the cladogram toward hook characteristics. Because the amount of required homoplasy was high when hook ratios were incorporated, we excluded these series from the analysis.

Further, hook pairs 3 and 4 have obviously longer proximal expansions of the shank than those of the remaining hook pairs in the outgroups and all but 4 ingroup species (*Anacanthorus amazonicus* sp. n., *A. prodigiosus* sp. n., *A. mastigophallus* Kritsky, Boeger, and Van Every, 1992, *A. gravihamulatus* sp. n.). Although the original descriptions of these 4 species do not indicate differences in the proximal expansion of the respective hook pairs, reexamination of the haptors confirms that hook pairs 3 and 4 are subtly larger than the remaining pairs. We consider this character to be symplesiomorphic for the ingroup and do not include it in the phylogenetic analysis.

PARASITE PHYLOGENY: The cladogram depicting phylogenetic relationships of the *Anacanthorus* species parasitizing 10 serrasalmid species from the central Amazon is presented in Figure 70. The consistency index (CI = 76.2%) was the highest obtained for hypotheses produced through the PAUP anaylsis utilizing the 12 homologous series. Monophyly of the ingroup is supported by 2 synapomorphies (character-state changes 1, 2): a cirrus with a tendency to curl into J-shaped to coiled configurations and an accessory piece nonarticulated to the cirral base. Character-state changes 3–11 represent symplesiomorphies for the ingroup (see character analysis).

Development of the cirral "feather" is a synapomorphy for the clade containing *Anacanthorus beleophallus* Kritsky, Boeger, and Van Every, 1992, and its 7-species sister group. The cladogram indicates that the ancestral state (character-state change 22) exhibited by *A. beleophallus* is an intermediate step in the full development of the "feather" as found in all but 1 of the remaining species in the clade. Even though a secondary loss of the "feather" has occurred in *A. cinctus* sp. n., the sister relationship of *A. cinctus* and *A. crytocaulus* sp. n. is strengthened by the derived morphology of the subterminal expansion of the accessory piece (Figs. 20, 67, 70).

HOST PHYLOGENY: One tree (Fig. 71) depicting phylogenetic relationships of the 10 serrasalmid hosts with a consistency index (CI = 71.4%) was produced through PAUP analysis using the matrix from parasite data. The positions of *Serrasalmus spilopleura* and species of *Pristobrycon* in the cladogram indicate that these genera are paraphyletic.

Discussion

In order to minimize effects of geographic and environmental variation on parasite communities (see Boeger and Kritsky, 1988), the species of *Anacanthorus* used in this study were purposely limited to those occurring in the central Amazon near Manaus. As a result, 5 previously described species from *Pygocentrus nattereri* were not included: *Anacanthorus maltai* and *A. rondonensis* reported and described by Boeger and Kritsky (1988) from the Brazilian state of Rondônia; and *A. anacanthorus, A. brazilensis,* and *A. neotropicalis* collected from aquarium hosts by Mizelle and Price (1965) in the United States. Boeger and Kritsky (1988) suggest that host specimens of the latter 3 species may have been misidentified, which limits the value of their parasites for coevolutionary studies.

The species of *Anacanthorus* infesting piranha in the central Amazon appear to form a monophyletic group defined by 2 synapomorphies: a cirrus with a tendency to curl and a nonarticulated accessory piece and cirrus. *Anacanthorus hoplophallus, A. pedanophallus, A. spinatus,* and *A. stagmophallus,* all described by Kritsky et al.

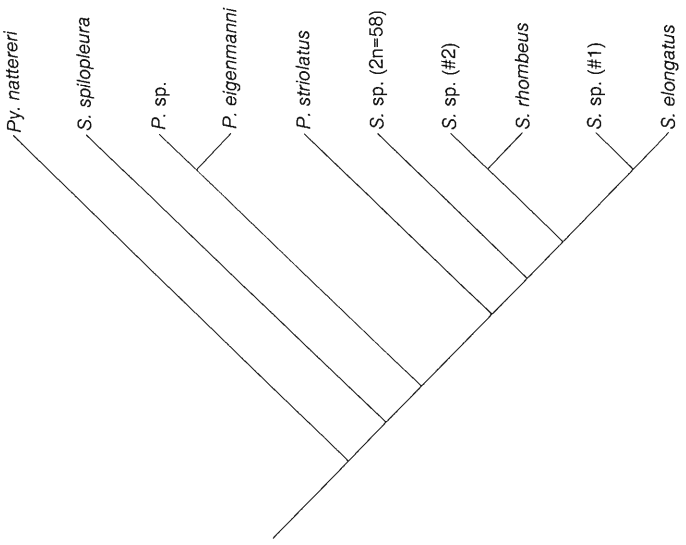


Figure 71. Cladogram depicting evolutionary relationships of 10 piranha species from the central Amazon based on their parasite fauna. *S.* = *Serrasalmus, P.* = *Pristobrycon, Py.* = *Pygocentrus.*

(1992) from *Myleus rubripinnus,* and an undescribed species of *Anacanthorus* from *Metynnis* sp. (Kritsky, unpubl.) also may have their origins within our ingroup. Since 1 objective of this study was to examine phylogeny and coevolution of the Anacanthorinae infesting *Pygocentrus, Pristobrycon,* and *Serrasalmus* (the 3 terminal serrasalmid genera of Machado-Allison, 1983), these 5 species were not included in the analysis. Further, our collections did not include any species from the potential host genus *Pygopristis,* which Machado-Allison (1983) places as sister to the 3 genera examined herein. The species of *Anacanthorus* from these and other serrasalmid genera (*Utiaritichthys, Acnodon,* and *Mylesinus,* and possibly *Piaractus*) also will likely fall within our ingroup and collectively provide an important model for studies on coevolution and biogeography of the entire Serrasalmidae.

Our hypothesis on phylogenetic relationships of *Anacanthorus* reveals several polychotomies (Fig. 70). These points of nonresolution may be attributable to a lack of informative homologous series for the ingroup species. However, it is possible that these unresolved nodes reflect historical geologic and climatic events that fragmented an ancestral distribution producing isolated populations in each of which speciation of the parasites could have occurred.

Considerable data exist to support periodic habitat changes in South America as a consequence of Quaternary climatic cycles (Cracraft and Prum, 1989). Although Weitzman and Weitzman (1982) question whether the evolution of higher taxa of Amazonian freshwater fishes corresponds to Pliocene and Pleistocene climatic events (Refugia), they suspect that these events may have been important in evolution at the minor generic and species levels. If the periodic drying and wetting of the Amazon Basin with consequent development of refugia played a role in fish speciation in the Neotropics (Weitzman and Weitzman 1982), the anacanthorine fauna could also have coevolved and speciated along with their hosts. Since refugia theory (Haffer, 1982 and others) assumes fragmentation of ancestral distributions, it could in part explain the unresolved topology of the parasite cladogram.

An alternative to the refugia theory that could also explain the unresolved nodes in our cladogram has recently been put forth by Frailey et al. (1988). The existence of a recent freshwater lake, Lago Amazonas, over the whole of the Amazon Basin may have provided a significant speciation mechanism not typically provided in a riverine system. Species diversity among Amazonian fishes and their parasites may be a result of la-

custrine resource partitioning, similar to that proposed to explain cichlid diversity in some African lakes (Lowe-McConnell, 1987) and Pliocene diversity in Lake Idaho (Smith, 1975). This single event of a "Lago Amazonas" could account for the evolution of several fish species from a single ancestor with the coinciding parasite fauna paralleling these speciation events.

Brooks (1979) suggests that coevolving hosts and parasites have experienced a common set of historical isolating events that may be reflected by occurrences and distributions of extant parasites on their hosts. He suggests 3 possible scenarios from these events. In the first, the parasites speciate while their hosts do not, which is reflected by extant sister species of parasites occurring on the same host. In his second scenario, the hosts speciate and parasites do not, resulting in the same extant species of parasite occurring on closely related hosts. In the third scenario, both hosts and parasites speciate, with the scenario being expressed by extant sister species of parasites occurring on sister host species. Our cladogram of *Anacanthorus* suggests that at least 2 of these 3 scenarios were involved during the evolutionary history of the ingroup. The sister relationships of *A. lasiophallus, A. crytocaulus,* and *A. cinctus* spp. n. and that of *A. thatcheri* Boeger and Kritsky, 1988, and *A. stachophallus* Kritsky, Boeger, and Van Every, 1992, are best explained by Brook's (1979) first scenario. Brook's (1979) second hypothesis is evident by several examples of closely related hosts harboring the same *Anacanthorus* species (see Figs. 1, 71). The third scenario may have also been involved in the evolution of the ingroup, but direct evidence from our data may be masked by the large, unresolved node in our cladogram. In any case, interpretation of coevolutionary relationships from our parasite cladogram requires explanation involving numerous instances of dispersal and/or extinction. However, the lack of an independently derived host phylogeny at the species level clearly limits the extent to which we can determine coevolutionary extinction and dispersal events.

While the generic relationships evident in our host cladogram (Fig. 71) generally support those offered by Machado-Allison (1983) for the genera *Pygocentrus, Pristobrycon,* and *Serrasalmus,* our host hypothesis suggests that the latter 2 are paraphyletic. Paraphyly of *Pristobrycon* was also suggested by Machado-Allison et al. (1989, Fig. 18B), who considered *P. striolatus* to lack a sister group relationship with any other members of the genus. It is clear that future tests of these emerging and possibly competing hypotheses on host evolution are necessary before the evolutionary history of the Serrasalmidae becomes clear.

Anacanthorus sciponophallus sp. n., *A. jegui* sp. n., and *A. xaniophallus* Kritsky, Boeger, and Van Every, 1992, occur on more than 1 host species as different morphotypes (see Figs. 43, 47, 51 this study; figs. 57–59, 118, 122 in Kritsky et al., 1992). Similarly, slight morphologic differences exist between specimens of *A. serrasalmi* sp. n. collected from different hosts. These terminal taxa with distinct morphologic forms may comprise collapsed clades composed of very closely related species. If this is the case, each clade could provide individual and independent tests of host relationships.

Although preliminary, this study demonstrates that the Anacanthorinae, and the Monogenoidea in general, provide useful models for the study of biogeography and coevolution in the Neotropics. However, caution should be used when interpreting coevolutionary relationships proposed from our parasite data. A number of hosts in our collections harbor distantly related *Anacanthorus* species, and O'Grady and Deets (1987) state that the use of inclusive ORing may give rise to phylogenetic inconsistencies when this occurs. In addition, host material may have been insufficient to ensure that all parasite species capable of infesting a host were found. Ideally, future studies to test hypotheses proposed herein would involve examination of parasites from a greater number of host specimens and species from a larger geographic area, utilization of other monogenoidean taxa, and incorporation of homologous series of host features into the matrix derived from the parasite cladogram.

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Addendum

Parasite–Host List of *Anacanthorus* Species*

SERRASALMIDAE
SERRASALMINAE

1. *Anacanthorus amazonicus* Van Every and Kritsky, 1992–*Serrasalmus rhombeus* (Linnaeus) (type); *Serrasalmus* sp. (2 of Jégu); *Pristobrycon striolatus* (Steindachner).
2. *Anacanthorus anacanthorus* Mizelle and Price, 1965–*Pygocentrus nattereri* Kner.
3. *Anacanthorus beleophallus* Kritsky, Boeger, and Van Every, 1992–*Pristobrycon eigenmanni* (Norman).
4. *Anacanthorus brazilensis* Mizelle and Price, 1965–*Pygocentrus nattereri* Kner.
5. *Anacanthorus cinctus* Van Every and Kritsky, 1992–*Pristobrycon striolatus* (Steindachner).
6. *Anacanthorus cladophallus* Van Every and Kritsky, 1992–*Serrasalmus spilopleura* Kner.
7. *Anacanthorus crytocaulus* Van Every and Kritsky, 1992–*Pristobrycon striolatus* (Steindachner).
8. *Anacanthorus gravihamulatus* Van Every and Kritsky, 1992–*Serrasalmus rhombeus* (Linnaeus) (type); *Serrasalmus* sp. (2 of Jégu); *Pristobrycon eigenmanni* (Norman).
9. *Anacanthorus jegui* Van Every and Kritsky, 1992–*Serrasalmus rhombeus* (Linnaeus) (type); *S. spilopleura* Kner; *Serrasalmus* sp. (2 of Jégu); *Serrasalmus* sp. (2n = 58); *Pristobrycon eigenmanni* (Norman); *Pristobrycon* sp.
10. *Anacanthorus lasiophallus* Van Every and Kritsky, 1992–*Pristobrycon striolatus* (Steindachner).
11. *Anacanthorus lepyrophallus* Kritsky, Boeger, and Van Every, 1992–*Serrasalmus elongatus* Kner (type); *Serrasalmus* sp. (1 of Jégu); *Serrasalmus* sp. (2n = 58).
12. *Anacanthorus maltai* Boeger and Kritsky, 1988–*Pygocentrus nattereri* Kner.
13. *Anacanthorus mastigophallus* Kritsky, Boeger, and Van Every, 1992–*Pristobrycon eigenmanni* (Norman).
14. *Anacanthorus mesocondylus* Van Every and Kritsky, 1992–*Serrasalmus elongatus* Kner (type); *S. rhombeus* (Linnaeus); *S. spilopleura* Kner; *Serrasalmus* sp. (1 of Jégu); *Serrasalmus* sp. (2 of Jégu); *Pristobrycon eigenmanni* (Norman); *Pristobrycon* sp.
15. *Anacanthorus neotropicalis* Mizelle and Price, 1965–*Pygocentrus nattereri* Kner.
16. *Anacanthorus palamophallus* Kritsky, Boeger, and Van Every, 1992–*Pristobrycon eigenmanni* (Norman).
17. *Anacanthorus periphallus* Kritsky, Boeger, and Van Every, 1992–*Serrasalmus* sp. (2n = 58) (type); *Serrasalmus* sp. (1 of Jégu).
18. *Anacanthorus prodigiosus* Van Every and Kritsky, 1992–*Serrasalmus elongatus* Kner (type); *S. rhombeus* (Linnaeus); *Serrasalmus* sp. (1 of Jégu); *Serrasalmus* sp. (2 of Jégu).
19. *Anacanthorus ramosissimus* Van Every and Kritsky, 1992–*Serrasalmus elongatus* Kner.
20. *Anacanthorus reginae* Boeger and Kritsky, 1988–*Pygocentrus nattereri* Kner.
21. *Anacanthorus rondonensis* Boeger and Kritsky, 1988–*Pygocentrus nattereri* Kner.
22. *Anacanthorus scapanus* Van Every and Kritsky, 1992–*Serrasalmus spilopleura* Kner.
23. *Anacanthorus sciponophallus* Van Every and Kritsky, 1992–*Serrasalmus elongatus* Kner (type); *S. rhombeus* (Linnaeus); *S. spilopleura* Kner; *Serrasalmus* sp. (1 of Jégu); *Serrasalmus* sp. (2 of Jégu); *Serrasalmus* sp. (2n = 58).
24. *Anacanthorus serrasalmi* Van Every and Kritsky, 1992–*Serrasalmus rhombeus* (Linnaeus) (type); *S. elongatus* Kner; *Serrasalmus* sp. (2 of Jégu); *Serrasalmus* sp. (2n = 58); *Pristobrycon* sp.
25. *Anacanthorus stachophallus* Kritsky, Boeger, and Van Every, 1992–*Pygocentrus nattereri* Kner.
26. *Anacanthorus thatcheri* Boeger and Kritsky, 1988–*Pygocentrus nattereri* Kner.
27. *Anacanthorus xaniophallus* Kritsky, Boeger, and Van Every, 1992–*Pristobrycon eigenmanni* (Norman) (type); *Pristobrycon* sp.

MYLEINAE

28. *Anacanthorus hoplophallus* Kritsky, Boeger, and Van Every, 1992–*Myleus rubripinnus* (Mueller and Troschel).
29. *Anacanthorus paraspathulatus* Kritsky, Boeger, and Van Every, 1992–*Mylossoma duriventris* (Cuvier).
30. *Anacanthorus pedanophallus* Kritsky, Boeger, and Van Every, 1992–*Myleus rubripinnus* (Mueller and Troschel).
31. *Anacanthorus spathulatus* Kritsky, Thatcher, and Kayton, 1979 (syn. *A. spatulatus* Kritsky et al., 1979, a misspelling)–*Colossoma bidens* (Spix) (type); *C. macropomum* (Cuvier).
32. *Anacanthorus spinatus* Kritsky, Boeger, and Van Every, 1992–*Myleus rubripinnus* (Mueller and Troschel).
33. *Anacanthorus stagmophallus* Kritsky, Boeger, and Van Every, 1992–*Myleus rubripinnus* (Mueller and Troschel).

CATOPRIONINAE

34. *Anacanthorus catoprioni* Kritsky, Boeger, and Van Every, 1992–*Catoprion mento* (Cuvier).

CHARACIDAE
CHARACINAE

35. *Anacanthorus dipelecinus* Kritsky, Boeger, and Van Every, 1992–*Roeboides myersii* Gill.

BRYCONINAE

36. *Anacanthorus acuminatus* Kritsky, Boeger, and Van Every, 1992–*Triportheus angulatus* (Spix) (type); *T. elongatus* (Guenther); *T. albus* Cope.
37. *Anacanthorus alatus* Kritsky, Boeger, and Van Every, 1992–*Triportheus albus* Cope (type); *T. elongatus* (Guenther).

* Host classification is based on Géry (1977; *Characoids of the World.* T. F. H. Publications, Inc., Neptune City, New Jersey, 672 pp.). *Anacanthorus* species are listed alphabetically according to families and subfamilies of their hosts.

38. *Anacanthorus andersoni* Kritsky, Boeger, and Van Every, 1992–*Triportheus angulatus* (Spix).
39. *Anacanthorus bellus* Kritsky, Boeger, and Van Every, 1992–*Triportheus albus* Cope (type); *T. elongatus* (Guenther); *Triportheus* sp.
40. *Anacanthorus brevis* Mizelle and Kritsky, 1969–*Brycon melanopterus* (Cope).
41. *Anacanthorus calophallus* Kritsky, Boeger, and Van Every, 1992–*Triportheus elongatus* (Guenther).
42. *Anacanthorus carinatus* Kritsky, Boeger, and Van Every, 1992–*Triportheus angulatus* (Spix).
43. *Anacanthorus chaunophallus* Kritsky, Boeger, and Van Every, 1992–*Triportheus angulatus* (Spix).
44. *Anacanthorus chelophorus* Kritsky, Boeger, and Van Every, 1992–*Triportheus angulatus* (Spix) (type); *Triportheus* sp.
45. *Anacanthorus colombianus* Kritsky and Thatcher, 1974–*Salminus affinis* Steindachner (type) (also *Tilapia mossambica* (Peters), Cichlidae [accidental]).
46. *Anacanthorus cornutus* Kritsky, Boeger, and Van Every, 1992–*Triportheus angulatus* (Spix).
47. *Anacanthorus cuticulovaginus* Kritsky and Thatcher, 1974–*Salminus affinis* Steindachner.
48. *Anacanthorus elegans* Kritsky, Thatcher, and Kayton, 1979–*Brycon melanopterus* (Cope).
49. *Anacanthorus euryphallus* Kritsky, Boeger, and Van Every, 1992–*Triportheus angulatus* (Spix) (type); *T. elongatus* (Guenther); *T. albus* Cope.
50. *Anacanthorus formosus* Kritsky, Boeger, and Van Every, 1992–*Triportheus elongatus* (Guenther) (type); *Triportheus* sp.
51. *Anacanthorus furculus* Kritsky, Boeger, and Van Every, 1992–*Triportheus elongatus* (Guenther).
52. *Anacanthorus glyptophallus* Kritsky, Boeger, and Van Every, 1992–*Triportheus angulatus* (Spix).
53. *Anacanthorus kruidenieri* Kritsky, Thatcher, and Kayton, 1979–*Brycon melanopterus* (Cope).
54. *Anacanthorus lygophallus* Kritsky, Boeger, and Van Every, 1992–*Triportheus angulatus* (Spix).
55. *Anacanthorus nanus* Kritsky, Boeger, and Van Every, 1992–*Triportheus angulatus* (Spix).
56. *Anacanthorus pelorophallus* Kritsky, Boeger, and Van Every, 1992–*Triportheus elongatus* (Guenther).
57. *Anacanthorus pithophallus* Kritsky, Boeger, and Van Every, 1992–*Triportheus angulatus* (Spix).
58. *Anacanthorus quinqueramus* Kritsky, Boeger, and Van Every, 1992–*Triportheus albus* Cope (type); *T. elongatus* (Guenther); *Triportheus* sp.
59. *Anacanthorus ramulosus* Kritsky, Boeger, and Van Every, 1992–*Triportheus albus* Cope (type); *T. elongatus* (Guenther).
60. *Anacanthorus spiralocirrus* Kritsky, Thatcher, and Kayton, 1979–*Brycon melanopterus* (Cope).
61. *Anacanthorus strongylophallus* Kritsky, Boeger, and Van Every, 1992–*Triportheus elongatus* (Guenther).
62. *Anacanthorus tricornis* Kritsky, Boeger, and Van Every, 1992–*Triportheus elongatus* (Guenther) (type); *T. angulatus* (Spix).